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Study of five skin glands of the pronghorn (Antilocapra americana Ord)

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A STUDY OF FIVE SKIN GLANDS OF THE PRONGHORN

(*Antilocapra americana* Ord)

by

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INTRODUCTION

Mammalian scent glands are epidermal derivatives consisting of apocrine suboriferous and sebaceous glands. These glands have been reported in 15 mammalian orders and classified into approximately 40 different types (Mueller-Schwarze, 1967).

The morphology and occurrence of such glands in man have been well documented (Montagna, 1962), but for other species, the picture is less complete. Shaffer's (1940) monograph reviews the skin glands of mammals and their histological formation and is the most comprehensive work available.

Scent production on the head involves the frontal, orbital, occiptal, cheek, and snout glands. Quay (1962) described the angulus oris gland of microtines. Harvey and Rosenberg (1960) described the gland at the base of the ear of the pika and related the variability in size of this gland to age and sex differences. Dalquest and Werner (1954) found extensive glandular areas in the face skin of seven families of bats.

The limbs of mammals may show the tarsal, metatarsal, interdigital, forearm, and femoral glands. Quay (1955) described the tarsal, fore- and hindfoot interdigital glands of the caribou, and the tarsal, metatarsal, and the interdigital glands of the whitetail deer (1959).

Comparatively few glands are found in the trunk region of the body. These include the ventral and lateral glands of the shorttail shrew (Pearson, 1946; Eddie, 1938), the dorsal skin glands of various kangaroo rats, (Quay, 1953; 1954), a dorso-lumbar scent gland of the javilina (Epling, 1956), the specialized midventral sebaceous glandular area in Rattus exlans (Quay and Tomich, 1963), and the species-specific posterolateral glands in microtine rodents (Quay, 1968).

The glands located in the genital-anal region include the anal, perineal, preputial and caudal (Mueller-Schwarze, 1967).

Considerable work has been performed on the histology and the histochemistry of the different scent glands. Each gland appears to be unique in each species and in some ways, histologically different from others.

Discrepancies have appeared over the years as to the function of the scent glands. Pocock wrote in 1910: "That each scent tells its own tale to other members of the species, it is almost impossible to doubt; but what the tale may be, I am wholly unable to surmise." Today the functions are only speculations. Mueller-Schwarze (1967) attempted to classify the possible functions as:

I. Intraspecific communication

a. Social attraction and keeping groups together

(including maternal behavior, species and individual recognition);

b. Reproductive behavior including epigamic aggression;

c. Warning signals;

d. Territory marking;

II. Others

a. Defense;

b. Orientation inspire

I feel that insufficient evidence has been collected to completely omit thermoregulation or osmoregulation as a possible function.

Mueller-Schwarze (1967) purified an odorous substance of the tarsal gland of the blacktail deer and tested the reactions of fawns to various fractions of these secretions. One fraction released positive social responses "approach," "following," "shifting," and "locking" in the young females but "fear" reaction in males. The tarsal odors can also be distinguished by both sexes and by the different age classes of the deer.

Many scent glands demonstrate no seasonal change (Quay, 1953, 1959, 1963, 1968; Pearson, 1946). There is evidence, however, that some scent glands show seasonal variation in glandular size and activity, and that they appear to be secondary sex glands. Dryden and Conaway (1967) revealed that castration of both sexes of the musk

shrew, causes the postauricular sweat gland to atrophy and cease musk production in the males and some females. Implanting testosterone and estradiol into these castrates causes the sweat glands to resume activity and odor production in both sexes. Quay (1953) working with the kangaroo rat, reported that the peak of glandular activity of the dorsal glands of the male Dipodomus merriami and D. agilis coincides with the breeding season and he mentioned that it is likely to be related to the breeding behavior. D. herrmanni, D. deserti, and D. ordii, on the other hand, show little if any correspondence between breeding season and dorsal gland activity. This example illustrates interspecific variation. For moles, Eadie (1954) noted that the activity of sudoriferous glands on the head, chin, wrists, and venter of the Parascalops, Condylura, and Scalopus are correlated to some extent with age and breeding condition. The size of the cheek gland of the pika also varies with its reproductive state (Harvey and Rosenberg, 1960). In women, the activity of axillary apocrine glands possibly parallels the phases of the menstrual cycle (Loeschcke, 1925; Schaffer, 1926; Cavazzana, 1947). However, Klarr (1926) and Montagna (1962) claim that the axillary glands undergo no change corresponding to the menstrual role.

The role of the scent glands as secondary sex organs; their marked interspecific and intergeneric variations;

their changes with seasons, sex and age; the degree of glandular activities; and their behavioral functions remain controversial.

In the artiodactyls the glandular areas vary in location, histology, histochemistry, and function. This study was designed to clarify some of the confusion concerning glands of the Artiodactyla by investigating the pronghorn (Antilocarpa americana).

Pronghorn have 11 cutaneous glands, five of which are paired (Caton, 1877). All of the glands except the two that are located behind each hock were examined during this study. Early observations on the glands of the pronghorn were made by Richards (1829), Canfield (1848) and Bartlett (1865) as cited by Caton. Caton gave the first complete and documented description of the glands. The two fore- and hindfoot interdigital glands are located between the toes. Caton described the secreted odor as unpleasant and seeming to grow stronger with age; he also mentioned that the glandular activity appeared constant.

The paired subauricular glands, sometimes referred to as the cheek or post-mandibular gland, have been found only on bucks and are located beneath the ears, ventral and posterior to the eyes on the posterior portion of the cheeks. The gland is a dark-brown patch surrounded by lighter brown hairs and is elongated dorso-ventrally. It becomes enlarged and actively secretes during the breeding

season. Caton (1877) and Seton (1929) reported that it seems to be associated with mating behavior.

Caton mentioned that the single median gland found on the back at the anterior edge of the white patch does not appear to be very active for its size.

The rump or ischiadic glands are found in the middle of each white rump patch. The glandular area can only be distinguished from the adjacent areas by the light-brown waxy substance located at the base of the hair stalks. Seton (1929) proposed that this gland may function as an "alarm system." He observed the following incident when a dog approached an antelope in the Washington Zoo. "All the long white hairs of the rump patch were raised with a jerk that made them flash in the sun. Each grazing antelope saw the flash, repeated it instantly, and raised its head to gaze in the direction toward which the first was looking. At the same time, I noticed on the wind a peculiar musky smell--a smell that certainly came from the antelope--and was no doubt an additional warning." Seton (op. cit.) dissected and studied the rump patch. He noted that the hairs at the upper part of the patch were about four inches long, grading to the center, and less than two inches long at the lower part. All the snow-white hairs were normally lying down flat and pointed toward the rear. At the center of the patch among the roots of the hair he found that the rump gland produced fluid having a strong

musky smell. He noted a broad sheet of muscular fibers on the underside of the skin. These were thickest at the center beneath the gland. He thought that when the antelope becomes frightened, the contracting muscles would instantly spread the rump patch radially into "great white blooming twin chrysanthemums," more or less flattened at the center, causing the glands to secrete the musky odor.

All the glands mentioned secrete a waxy substance, milky-tan in color and with a pungent odor. Some secrete more copiously than others. Caton (1877) suggested that the pungent odor, particularly from the rump gland, helped to protect the antelope from insects. Seton (1929) believed that the primary use of the rump gland was for communication within the species.

The rump and subauricular glands of males killed each month; the rump and subauricular glands of three castrated males; the rump and subauricular skin of a doe; the fore- and hindfoot interdigital glands and median gland from one male killed in January; and a few skin samples were available for my inspection.

From this material I attempted: to describe the basic anatomy and histology of the five glands and regular skin; to determine any seasonal variations of the glands; to compare the histology of the female and male rump gland for any significant differences; to look for remnants of a subauricular gland in the cheek skin of the doe antelope;

to compare the histology, histochemistry and prescribed measurements of the apocrine and sebaceous zones of the subauricular and rump glands; and, to determine whether the increase in the activity of the subauricular gland during the rutting season is related to increase in testicular activity.

MATERIALS AND METHODS

Field Methods and Materials

Monthly specimens of the subauricular and rump glands were collected from adult pronghorn bucks by a former zoology graduate, Ernest Roney, on the National Bison Range, Moeise, Montana, in 1961-1962. (Table I). He also castrated several young bucks, two of which were sacrificed (specimens H3082 and H3089) and their skin glands preserved. The ages of the castrates are unknown. A fawn (H3561) was castrated at two days of age and was sacrificed four years later (Table II).

With the assistance of Dr. Bart O'Gara, two additional pronghorns were collected from the Bison Range. One animal was collected in February to complete the monthly sequence of the subauricular and rump glands and another animal was collected in January. The fore- and hindfoot interdigital glands and median gland were also removed from this January antelope. Inasmuch as the rump and subauricular glands collected by Roney in December and January were from yearling bucks, skin glands from a mature buck were collected for purposes of comparison.

The recently collected glands were immediately fixed in AFA, Bouins fixative or buffered formalin for seven days, and then transferred to 70% ethanol for storage. The buck's testes were removed and fixed for a study by O'Gara and me on the seasonal changes in testicular activity and size.

TABLE I

Male and Female Pronghorns Collected

Sample No.	Date Collected	Collector	Age (years and months)
Male Pronghorns			
62-1	Jan. 27, 1962	Roney	1-7
69-1	Jan. 21, 1969	Moy-O'Gara	8-7
68-2	Feb. 16, 1968	Moy-O'Gara	4-8
62-3	Mar. 31, 1962	Roney	2-9
62-4	Apr. 30, 1962	Roney	1-10
61-1	May 9, 1961	Roney	--
61-2	June 22, 1961	Roney	2-0
61-3	July 28, 1961	Roney	7-1
61-4	Aug. 30, 1961	Roney	2-2
61-5	Sept. 29, 1961	Roney	2-3
61-6	Oct. 27, 1961	Roney	3-4
61-7	Nov. 23, 1961	Roney	3-5
61-8	Dec. 15, 1961	Roney	1-6
Female Pronghorns			
68-10	Oct. 20, 1968	O'Gara	4-4

TABLE II

Castrated Male Pronghorns Collected

Sample No.	Date Castrated	Date Collected	Collector	Age (years and months)
H3082	May 9, 1961	Aug. 2, 1963	Roney	4-2
H3089	March 13, 1962	Aug. 2, 1963	Roney	---
H3561	June 11, 1961	Aug. 11, 1965	Wright	4-2

A doe antelope shot by O'Gara during the 1968 hunting season in Petroleum County, Montana, was used for comparison with the glands of the males.

The animals were aged by Dr. O'Gara on the basis of tooth wear (Dow and Wright, 1962). Two animals were not aged because the jaws could not be located (Tables I, II).

Laboratory Methods and Materials

The diameter of the rump glands, the greatest length and width of the subauricular gland, and the diameter of the median gland were grossly measured to the nearest 0.1 mm. The approximate surface area of the subauricular gland was determined by using $\frac{1}{4} \pi LW = A$, since the glandular area is in the shape of an ellipse. The various measurements made on the one fore- and hindfoot interdigital gland to the nearest 0.1 mm. are shown in Figure 1 and recorded in Appendix B.

To obtain a small tissue block from the center and most glandular area of the subauricular, an incision was made lengthwise from top to bottom (see Figure 2, A-B). At approximately the thickest point along the first incision, another cut was made widthwise (see Figure 2, C-D). Similar incisions were made along the diameter of the rump glands to expose the thickest glandular area. Glandular height and skin thickness were measured for the subauricular, rump, and the median glands to the nearest 0.01 mm. at their

Explanation of Figures

Figure 1. Lateral view of a dissected fore- or hindfoot interdigital gland. A through F represent the various measurements recorded for the interdigital glands. Measurement D refers to the diameter of the gland's orifice. Tissue blocks 1, 2 and 3 were removed and examined histologically.

Figure 2. Incisions A-B and C-D were made on the ventral surface of the subauricular gland to expose the center and the greatest glandular area. The tissue blocks for histological examination were removed at this point.

Figure 1

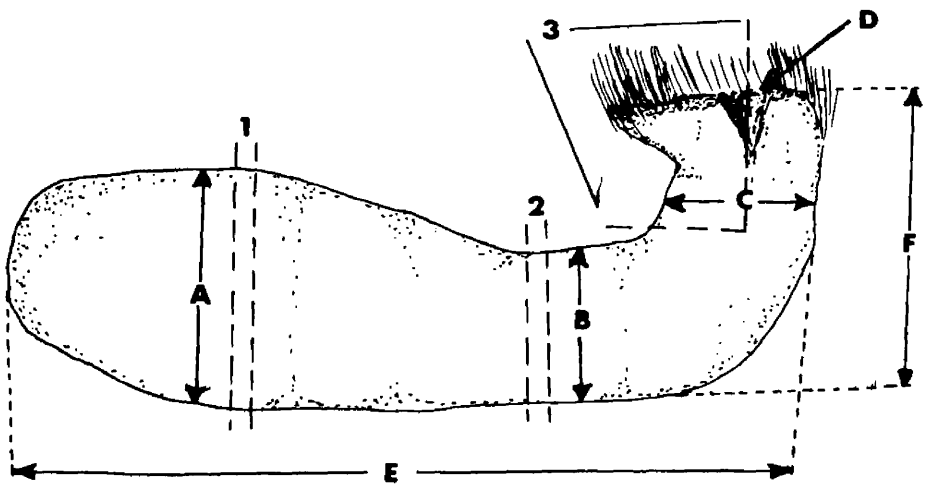
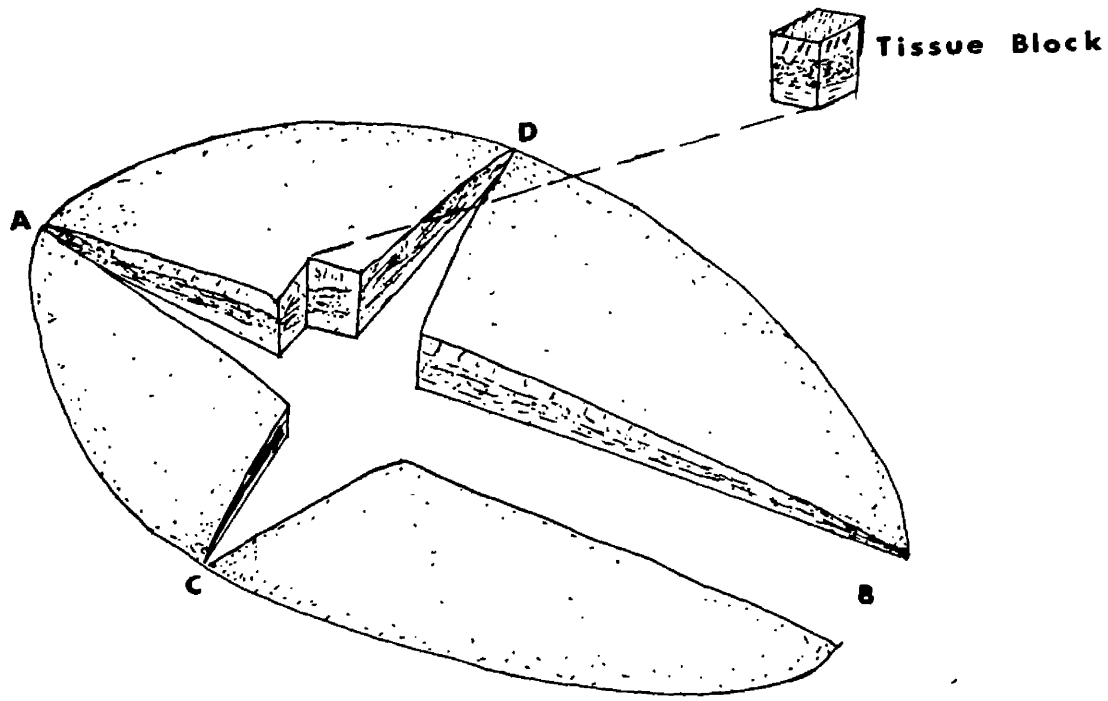


Figure 2



thickest point. Tissue blocks 1, 2, 3 (Figure 1) were dissected from the fore- and hindfoot interdigital glands for histological examination. All gross measurements were made with a fifteen cm. ruler, Vernier Calipers and Helios dial Calipus.

The tissue blocks were removed from the approximate center of the gland, dehydrated through an ethanol series, cleared overnight in methyl silicylate, washed briefly in toluene, and infiltrated in three two-hour changes of 56 degree paraffin. The long infiltration time was necessary because of the toughness of the elastic and collagenous tissue. The tissue blocks were oriented so that sections could be cut on the same plane as the hair root. Paraffin sections 10-12 μ in thickness were treated with the following techniques from Humason (1967).

1) Groat's variation of Weigert's Hematoxylin and Eosin Y

2) Heidenhains Iron Hematoxylin and Eosin Y

3) Mallory Heidenhains stain, a rapid one-step method for connective tissue

4) Luxol Fast Blue AFN for myelin

5) Turnbull Blue Method for ferrous iron

6) Periodic Acid-Schiff reaction without counter-stain for PAS positive reactions

7) Toluidine Blue for cell granules

8) Thionin for acid mucopolysaccharides

9) Ziel-Nielsen for cell granules

10) Aldehyde-Fuchsin for secretory granules

Sections cut 25-100 μ on a clinical freezing microtone were treated with Oil Red O and Sudan Black B to demonstrate lipids. Some of these sections were counterstained with Delafield's Hematoxylin.

The following glandular and cellular sizes of the subauricular and rump glands were measured with an ocular micrometer.

I. Measurements made at 100 X were: 1) thickness of the reticular zone, 2) thickness of the apocrine zone, 3) thickness of the sebaceous zone, 4) thickness of the inner collagenous zone, and 5) estimate of hair follicle depth to the nearest micron.

II. Measurements made at 400 X were the diameter of the hairs of the glands to the nearest micron.

III. Measurements made at 1000 X were: 1) thickness of the epidermis and the depth in numbers of nucleated cells, 2) diameters of the apocrine cell nuclei, 3) diameters of sebaceous basal cell nuclei, 4) diameters and lengths of myoepithelial cell nuclei, and 5) diameters of sebaceous storage vessicles of subauricular gland, if present.

To determine if seasonal proliferation of the subauricular or rump glands occur, the following measurements of apocrine tubules were made: 1) the lumen of apocrine

tubules, 2) the diameter of the apocrine tubules, and 3) apocrine cell heights. Sufficient measurements, approximately every other tubule, were recorded in order to calculate the means, standard deviation, and 95% confidence level of the standard error. These measurements are included in Figures 89-94 and are recorded in Appendix A.

RESULTS AND DISCUSSION

Subauricular Gland

Gross Description. The subauricular gland is a thickened area of the skin beneath the ear of male pronghorn antelopes. This elliptically-shaped gland ranges in size from approx. 3,100 sq. mm. in January to approx. 10,000 sq. mm. in July (Table III, Figures 3 to 6). The greatest development of the sebaceous and apocrine regions is at the center of the gland. There is a gradual transition from highly glandular in the center to the non-glandular periphery. This transition is not so evident in the quiescent gland from winter specimens (Figures 7 to 10). Gross measurements of the glandular area, the maximum skin-gland thickness and glandular thickness vary seasonally (Table II), reaching a maximum in June and July, and a minimum in December and January.

The hairs of the gland are darker and finer (approximate length 10-18 mm. and diameter of 100-180 μ). The darkest hairs are located near the center of the gland. The hairs swirl inward toward the center. At the base of the hair shaft, the color is grayish-brown, gradually turning to a dark brown shaft and brown to blackish at the tips. A few other light-colored and short (2-3 mm.) black hairs cover the surface of the gland. Milky-tan secretory globules can usually be seen on the hairs. During the summer months the hairs of the gland appear darker (Figures 7 to 10).

TABLE III

Gross Measurements of the Subauricular Glands

Month & Specimen Number		Approx. area of gland in sq.mm. $\frac{1}{4} \pi$ LW = A	Skin gland max. height in mm.	Max. glandular thickness in mm.
62-1	January	3,100	5.2	3.2
69-1	January	4,400	9.1	3.8
62-2	February	6,000	9.6	5.4
62-3	March	4,000	11.0	7.2
62-4	April	5,700	11.1	6.8
61-1	May	-----	11.9	6.8
61-2	June	6,300	13.0	9.2
61-3	July	10.000	13.4	7.4
61-4	August	-----	10.8	7.4
61-5	September	6,600	9.5	5.6
61-8	October	-----	10.2	3.2
61-7	November	-----	8.9	3.8
61-8	December	3,700	5.7	2.0

Some glands were not dissected entirely and their measurements were omitted.

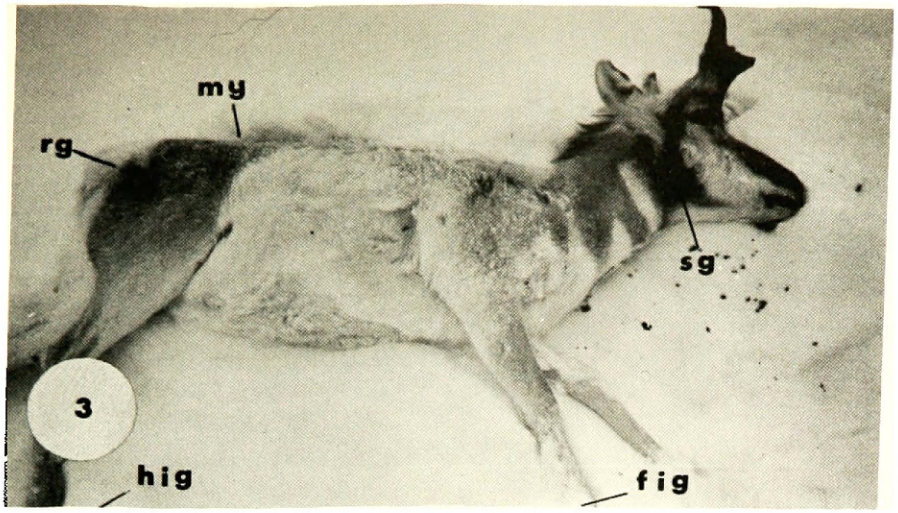
Explanation of Figures

Figure 3. Antelope 69-1 was photographed immediately after it was shot. This figure shows the location of the subauricular gland (sg), rump gland (g), median gland (mg), and fore- and hind interdigital gland (fig and hig).

Figure 4. The subauricular gland (sg) is located below the ear and posterior to the jaw. The short dark hairs of the gland are evident.

Figure 5. A close-up of the contrast and pattern of the hairs of the subauricular gland of antelope 69-1.

Figure 6. The rump gland of antelope 69-1 being dissected by Dr. O'Gara and myself. The animal was shot on the National Bison Range.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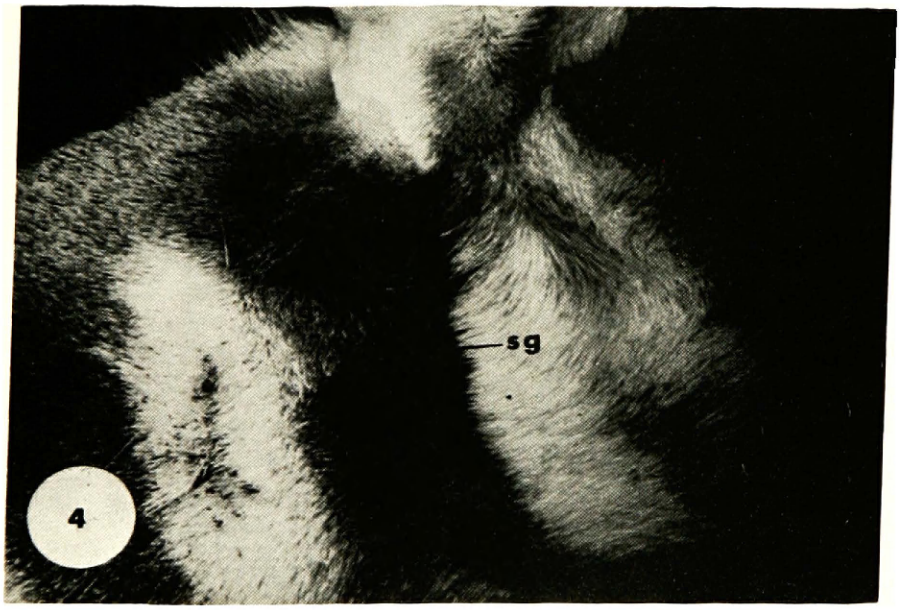

sg
4


5


6

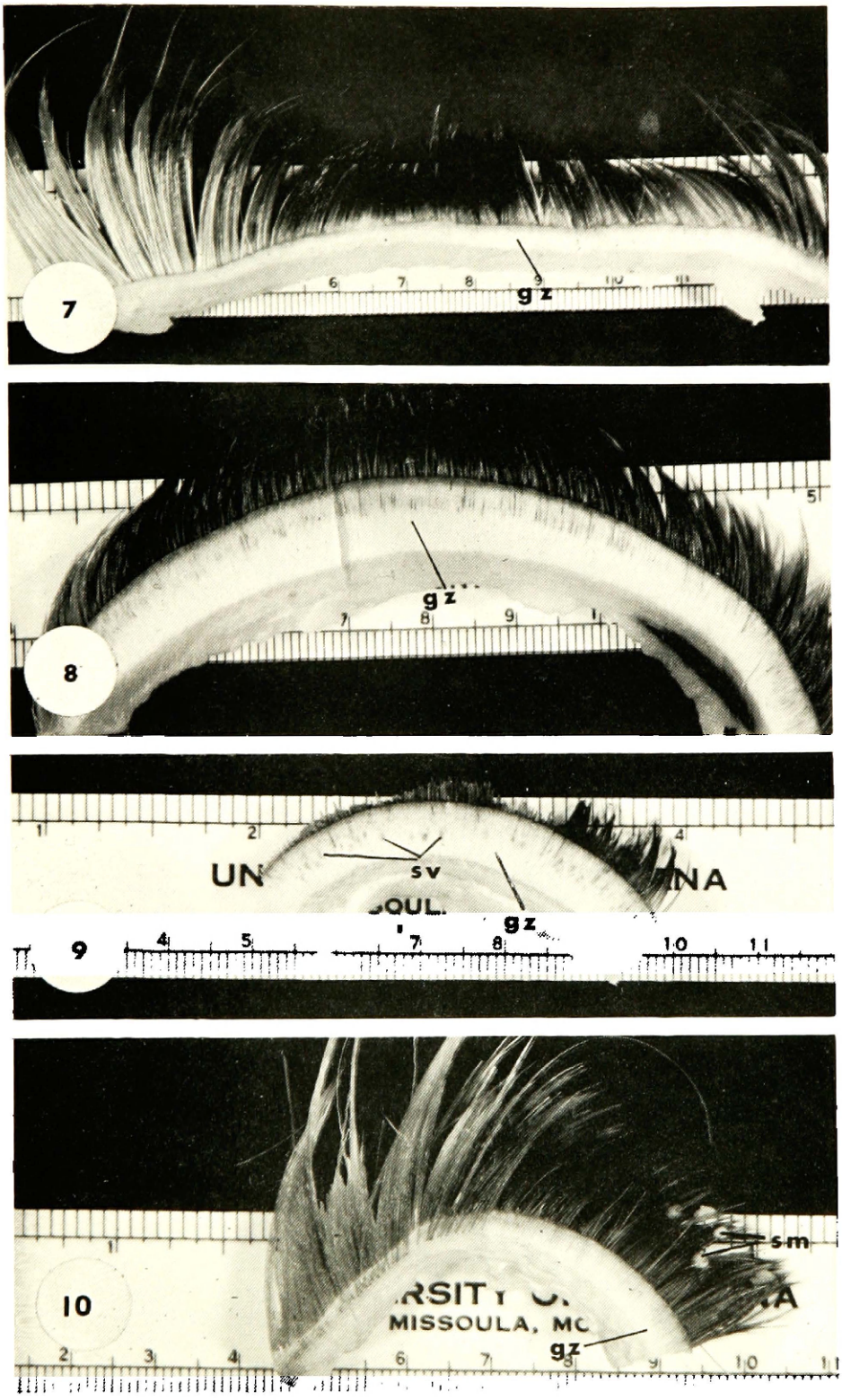
Explanation of Figures

Figure 7. A cross section through the center of the subauricular gland of January 69-1, shows the thin glandular zone (gz). Notice the length of the thin zone. Approx. 9/10 X.

Figure 8. A cross section through the subauricular gland of June 61-2, shows a thick, well-developed zone (gz). Approx. 11/10 X.

Figure 9. A segment of the cross section through the center of the subauricular gland 61-4, of August, shows a thick zone (gz) and numerous large storage sebaceous vessicles (sv) typical of this month. Approx. 11/10 X.

Figure 10. A segment of the cross section through the center of the subauricular gland 61-7, of November, shows a thinner zone (gz) and secretory material (sm) on the hairs. Approx. 11/10 X.


7
gz
8
gz
sv
gz
9
sm
10
gz

The adjacent hairs are twice as long and about twice the diameter of the glandular ones. These hairs are grayish to tan in color, and their base is always lighter than their shaft and tip.

Glandular Components. The subauricular gland is located in the epidermis and the dermis. Four different glandular zones are evident in the dermis: an outer zone which includes the papillary and reticular areas, a sebaceous zone, and apocrine zone, and an inner zone.

Epidermis. The depth of the epidermis seems to vary with the seasons (Table IV), and is thinnest during the winter months. In January the epidermis measures 10-30 μ and is 2-5 nucleated cells thick, but by June, it measures 60-140 μ and is 4-13 nucleated cells thick.

The epidermis thickens around each hair orifice and follows the hair follicle a short distance into the dermis.

The outer layer of the epidermis is the stratum disjunctum which is comprised of loosely arranged, dry cornified desquamated cells, 0-27 μ thick. Near the hair orifice, this layer obtains the greatest thickness. The underlying thin (0-6 μ) stratum corneum is difficult to distinguish from the stratum disjunctum except that the dead cells are more compact. The stratum granulosum is composed of one to two layers of elongated squamous cells, with nuclei measuring 7-10 μ in length. The thickest layer,

TABLE IV

Measurements of the Epidermis of the Subauricular Gland at 1000 X

Month & Sample Number		Approximate thickness of the epidermis, μ	Approximate Number of cells thick in the epidermis
62-1	January	10-30	2-5
69-1	January	15-45	2-5
68-2	February	10-30	2-5
62-3	March	27-80	4-8
62-4	April	35-75	3-8
61-1	May	30-75	3-8
61-2	June	60-140	4-13
61-3	July	19-70	3-7
61-4	August	20-70	3-9
61-5	September	25-40	2-6
61-6	October	15-35	2-5
61-7	November	-----*	---*
61-8	December	10-20	1-2

*These measurements could not be recorded because the epidermis had been shaven away when the tissue block was prepared.

the stratum germinativum, is 5-130 μ thick, and fluctuates significantly in different seasons. The polyhedral cells of this layer are somewhat round with a circular nuclei that measures 6-10 μ in diameter. Lying next to the dermis are the cylindrical basal cells which have ovoid nuclei measuring 6-14 μ in length. Melanin granules are found associated in this region, mostly congregated on the surface side of the cell's nuclei.

Outer Zone. Beneath the epidermis lies the thin papillary layer, a transitional layer between dermis and epidermis. This layer is composed of delicate, loosely arranged connective tissue which gives rise to the denser connective stroma of the reticular zone. This reticular area consists of bundles of collagenous with a few elastic fibers. In half of the glands, the fibers are arranged irregularly; in the others, it appears more or less parallel to the surface. The elastic fibers fill the gaps between the collagenous fibers and form a more condensed network. Numerous fibroblasts are found associated with the collagenous fibers. The reticular zone seems to become slightly thicker during the summer (Table V).

Histology of the Sebaceous Zone. Sebaceous glands, first described by Eichorn in 1826, are appendages of the hair follicles. Montagna (1962) mentioned that the size of the sebaceous glands often varies inversely with the size of the hair follicles with which they are associated. Since

TABLE V

Approximate Measurements of the Dermis of the Subauricular Gland at 100 X in mm.

Month	Reticular Zone	Sebaceous Zone	Apocrine Zone	Inner Zone	Hair Follicle Depth
January	.75	1.08	1.61	.90	1.6
January	.55	.55	1.20	1.30	1.6
February	.75	2.47	3.31	3.00+	2.9
March	.68	2.21	3.81	1.75	2.3
April	.70	2.11	4.03	1.25+	2.7
May	.75	2.82	3.77	2.55	2.8
June	1.25	3.25	5.33	3.05	4.1
July	.63	2.54	4.36	3.80	3.1
August	1.30	3.25	3.94	--*	4.0
September	.65	1.95	2.62	--*	--*
October	1.10	1.82	1.11	2.50	2.4
November	.90	1.24	1.50	1.50	2.5
December	.65	.78	.85	1.00	1.4

*The lower zone was accidently removed when the gland was trimmed.

the hairs of the subauricular gland are small, one would expect large sebaceous glands. This is the case. Sebaceous glands have been thoroughly reviewed in humans and other mammals (Montagna, 1962; Quay, 1955, 1959, 1963, 1965, 1968; and others). Quay (1955 and 1959) has described sebaceous glands of two artiodactyls, the whitetail deer and the caribou.

The sebaceous zone of the subauricular gland of the pronghorn lies beneath the reticular zone and undergoes cyclic changes (Table V). During the active summer period this area consists of tall, large pillars of holocrine sebaceous units called acini or aveoli (Figure 12). The acini are encapsulated by a basement lamina supported by a thin fibrillar connective tissue sheath. A network of collagenous and elastic fibers fill the space between the acini. A common excretory duct empties into the pilosebaceous canal near the neck of the hair follicle. This duct is lined by stratified squamous epithelium that is continuous with the walls of the pilosebaceous canal. Along the periphery of the acini are located undifferentiated ovoid and circular basal cells that resemble cells of the epidermis. Basal cells nearest the connective tissue sheath are more elongated. The nuclei of the basal cells measure from 4-6 μ in diameter. In the glandular acini, the central cells show centripetal enlargement, measure 10-20 μ in diameter, and have nuclei that measure 5-10 μ

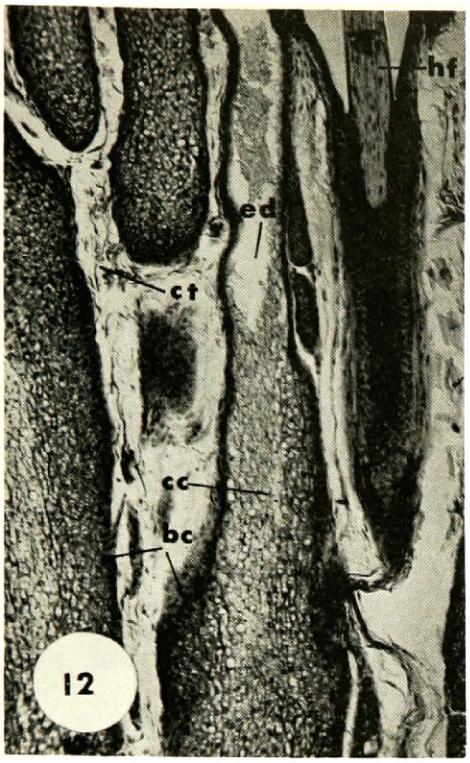
Explanation of Figures

Figure 11. The sebaceous acini of the subauricular gland 68-2 for February are stained with Sudan B. The center of the mature acini (ma) are stained deep black, as are the excretory ducts (ed) and pilosebaceous canal (pc). Hair follicle (hf). Sectioned at 30 μ. Approx. 84 X.

Figure 12. The sebaceous acini of subauricular gland 62-3 for March show the tall pillar arrangements of the acini. Small basal cells (bc) are along the periphery of the acini and in the center are the differentiating central cells (cc), which give rise to the excretory ducts (ed). Notice the hair follicle (hf) and the connective tissue (ct) around the acini. Approx. 84 X.

Figure 14. A closer view of an acini of subauricular gland 62-3 shows the small basal cells (bc) and the gradual accumulation of lipid vacuoles (lv) in the central cells (cc). Approx. 383 X.

Figure 15. Subauricular gland 61-1. The large nuclei of the central cells (cn) are surrounded by numerous large lipid vacuoles (lv). The smaller vacuoles (1) around the slightly differentiated cells combine with others to form large vacuoles (2). Approx. 842 X.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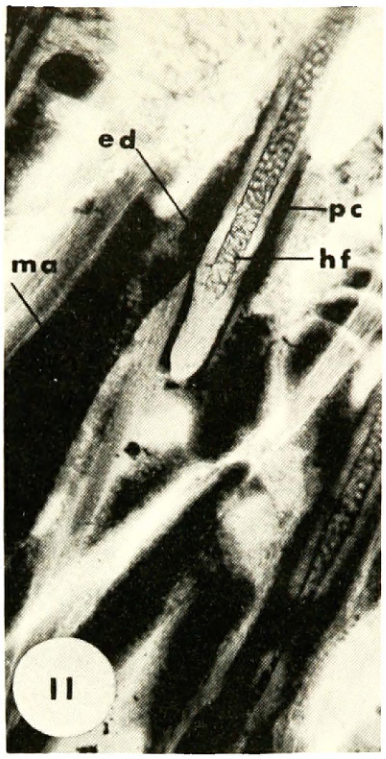
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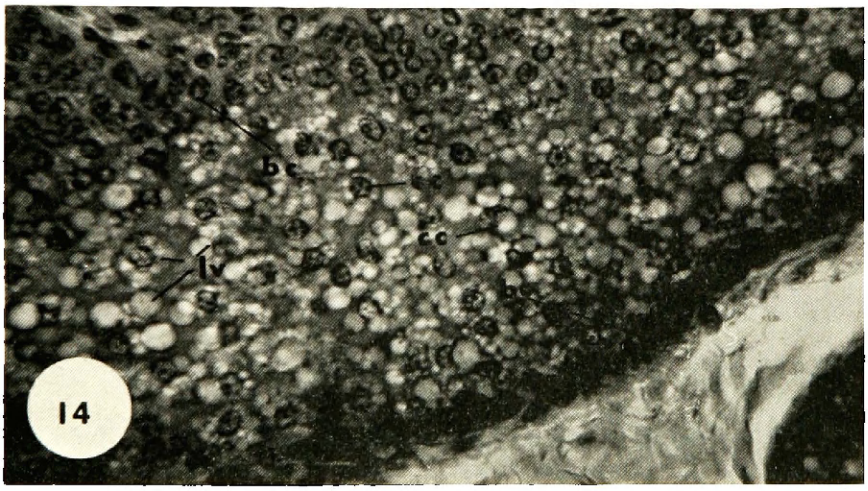
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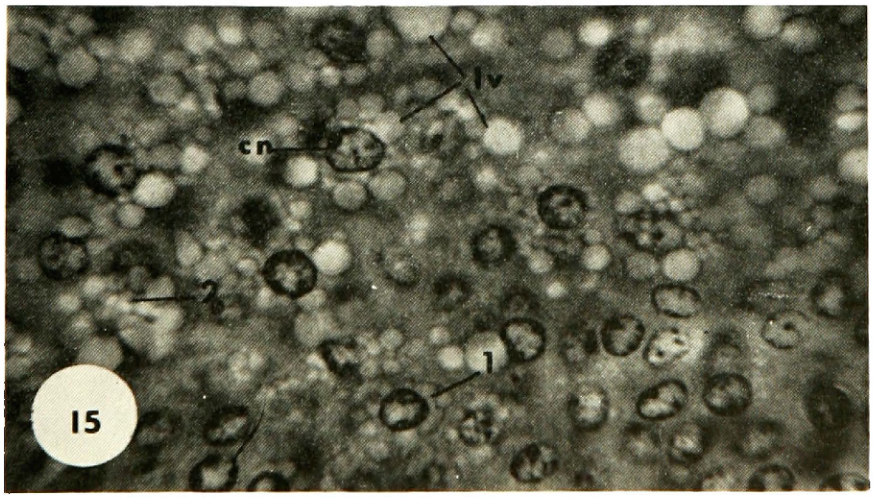
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in diameter. These cells are considerably larger than the basal cells. The central cells are often misshaped-polyhedral, moribound, and distended with lipid vacuoles (Figures 14 and 15). The mature acini and the ducts contain sebum, a substance composed of lipids and cell debris.

Secretory Process of the Sebaceous Gland. The minute lipid vacuoles, 3-6 μ in diameter, start to appear as the cells begin to differentiate along the periphery of the acinus. As these cells migrate centrally, their nuclei and lipid vacuoles gradually enlarge (Figures 14 and 15). The individual droplets become 10-20 μ in diameter. Cytolysis of the central cell is first evident by the large polyhedral nuclei and the accumulation of lipid droplets. The cell walls and nuclei then begin to distort, shrink, and disintegrate, and finally are incorporated into the sebum (Figure 19). I was unable to determine whether the sebum was secreted onto the surface by pressure flow or by milking action of arrector pili muscles.

Proliferation and Regression of the Sebaceous Gland. December and January are quiescent periods during which time many basal cells are found in the small, undifferentiated, lobulated acini (Figures 24 to 27). By February, the growth of the sebaceous gland commences by downward proliferation of the basal cells along the tip of the acini. Lateral buds form near the neck of the individual sebaceous units and expand out and downward, soon encroaching upon

nearby acini. The acini fuse and become larger. Small epithelial cells and fibroblasts adhere to and outline the periphery of the fused parts. The season of greatest glandular activity becomes apparent in the summer as the individual sebaceous acini are the largest, the differentiating cells along the periphery of the acini have great lipid accumulation, and immense sebum storage vessicles are present (Table VI). The storage vessicles are found in the lower portion of mature acini (Figures 16 to 20) and are formed by complete maturation or cytolysis of portions of the acini. Vessicles are lined by stratified squamous epithelium and by the sheath that encapsulates the acini (Figures 7 and 8). The ovoid vessicles are most numerous in August and measure from 200-900 μ at the largest width diameter. Smaller and less frequent vessicles are observed in June and September.

During September the sebaceous vessicles decrease in size and the loose connective tissue and fibroblasts begin to invade along the bottom portion of the acini, forming smaller sebaceous lobules (Figures 21, 22 and 23). The accumulation of lipid vacuoles within the central cells becomes considerably less (Figure 27). The continued invasion of numerous fibroblasts and connective tissue during the fall months form small undifferentiated branched units (Figures 25 and 26). Denser connective tissue immediately replaces the loose connective tissue (Figure 26).

TABLE VI

Estimation of the Activity of the Subauricular Activity

Month	Apocrine Activity	Sebaceous Activity
January	+	+
January	+	+
February	+	++
March	++	++
April	++	+++
May	+++	++
June	++++	+++
July	+++	+++
August	++++	++++
September	++	++
October	+	+
November	+	+
December	+	+

0 = no activity
\+ = poor activity
++ = moderate activity
+++ = active activity
++++ = extremely active activity

Apocrine Activity is determined by: the amount of cytoplasmic budding, the type of secretory epithelium, and the amount of secretory material in the lumen.

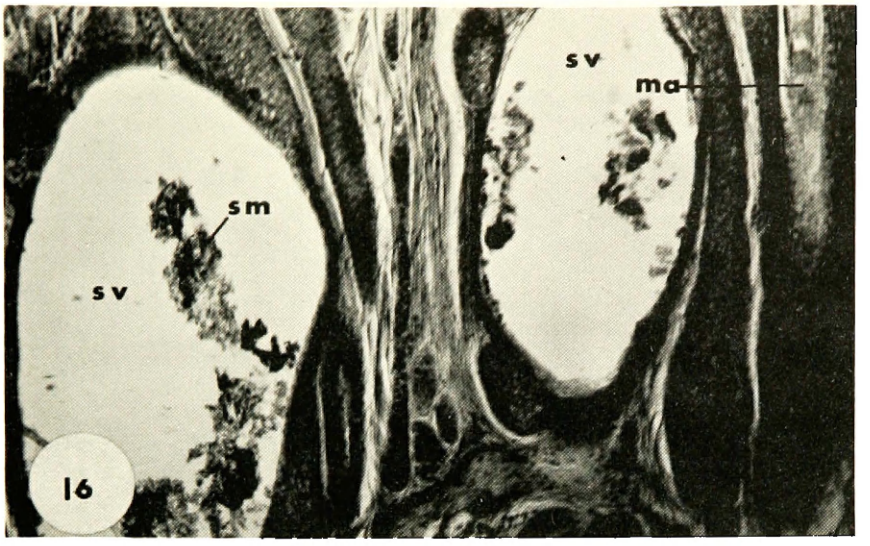
Sebaceous Activity is determined by: the size and maturation of the acini, the amount of sebum, and the differentiation of the peripheral and central cells.

Explanation of Figures

Figure 16. Large sebaceous storage vessicles (sv) are found in the August, 61-4 subauricular gland. They are an indication of the peak of sebaceous activity. Notice the mature acini (ma) along side the vessicles. Secretory material (sm). Approx. 84 X.

Figure 17. A few large vessicles (sv) are present in the June 61-2 subauricular gland. This vessicle is surrounded by mature sebaceous acini (ma). A thick basement membrane (bm) and stratified squamous epithelium encapsules most of the vacuole. Approx. 383 X.

Figure 18. The lining around the vessicle of subauricular gland 61-2 still shows some sebaceous cells (sc), that have not completely undergone cytolysis. Basement membrane (bm). Approx. 842 X.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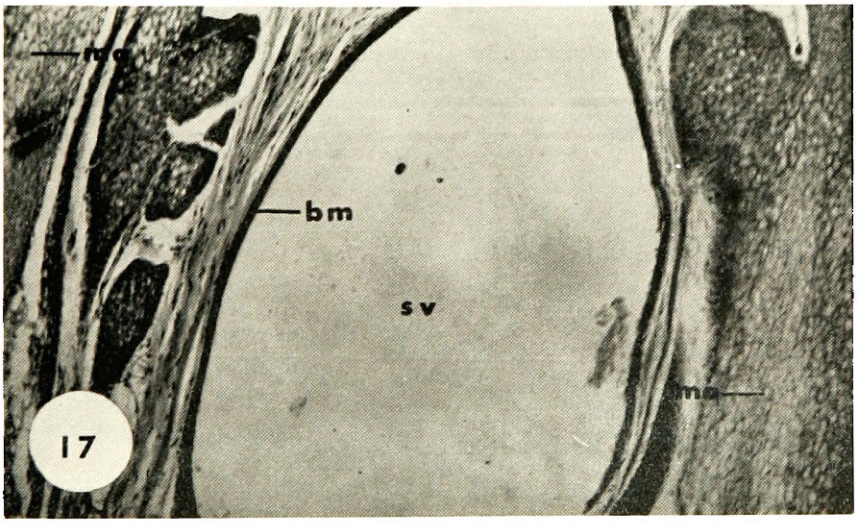
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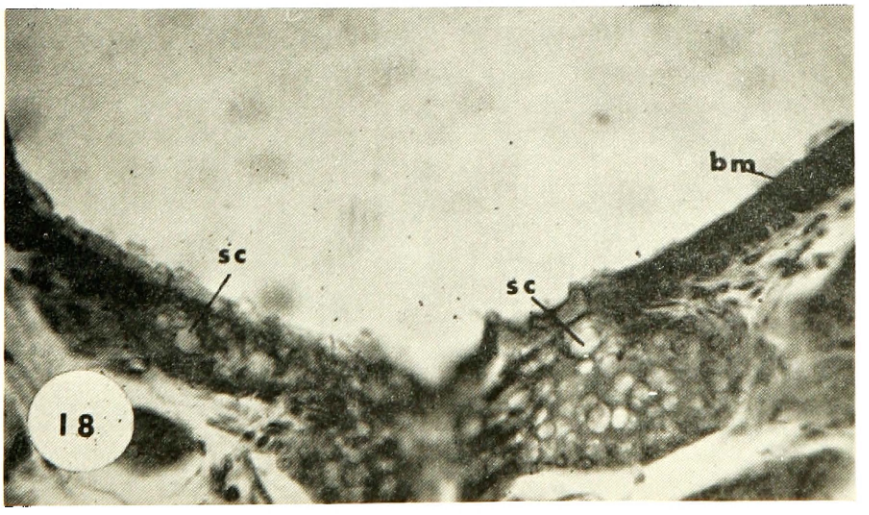
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Explanation of Figures

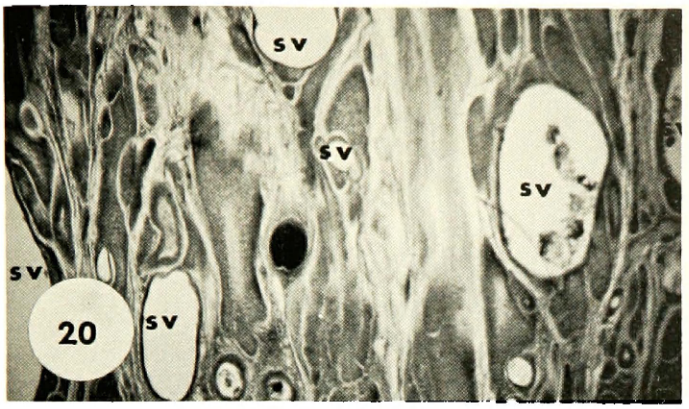
Figure 19. The sebaceous acini of the June 61-2 subauricular gland are quite mature. A few basal cells (bc) are along the periphery of the acini. Notice the large lipid vacuoles (lv), and the distored and disintegreting nuclei of the central cells (n). Approx. 842 X.

Figure 20. Numerous sebaceous storage vessicles (sv) are found in the mature August 61-4 subauricular gland. Approx. 34 X.

Figure 21. In September, subauricular gland 61-5, the sebaceous acini are smaller and more undifferentiated. Approx. 383 X.

Figure 22. Subauricular gland 61-5. Loose connective tissue (ct) and fibroblasts invade along the bottom portion of the sebaceous acini. Approx. 383 X.

Figure 23. Subauricular gland 61-5. Notice the invading connective tissue (ct) and fibroblasts. Basal cells become more numerous. Approx. 383 X.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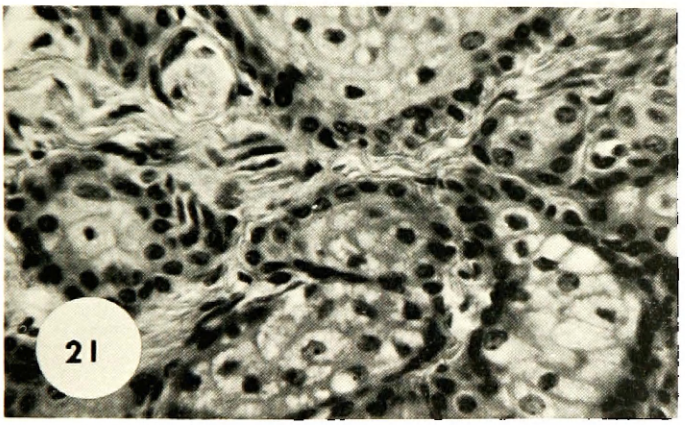
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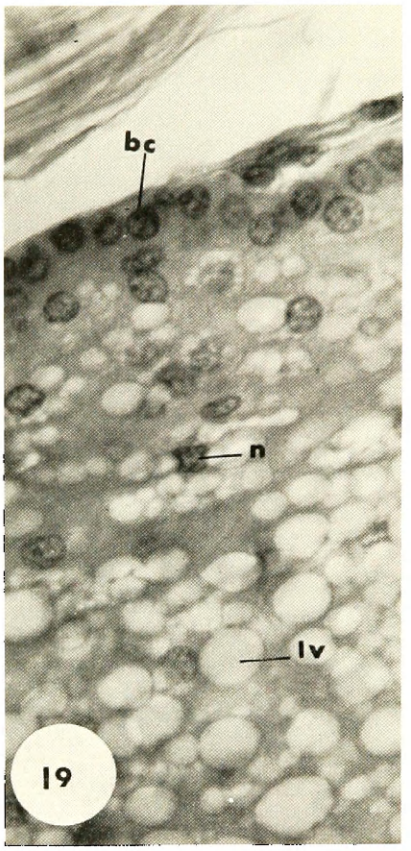
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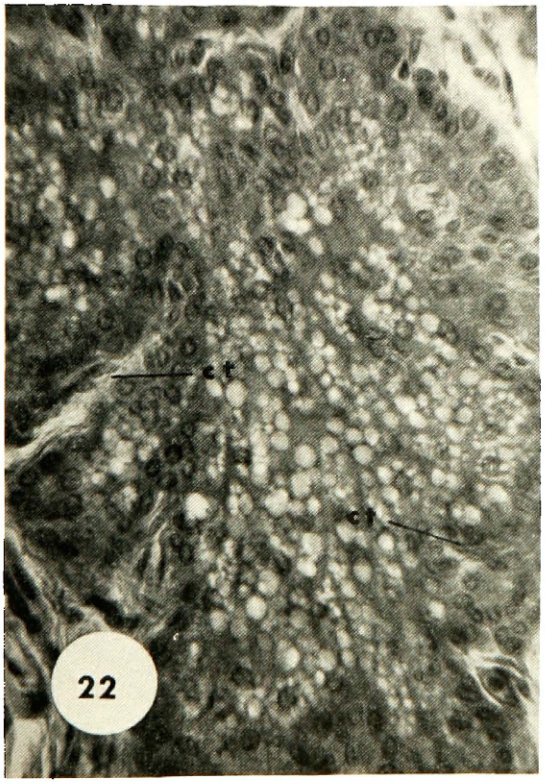
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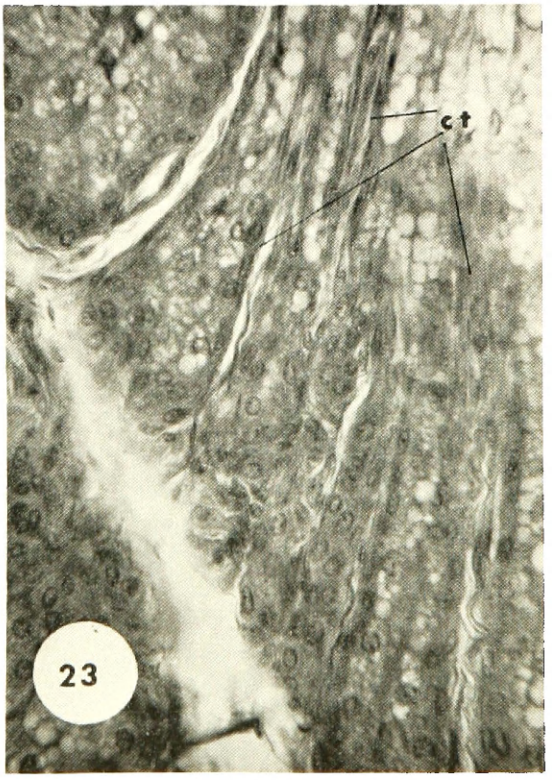
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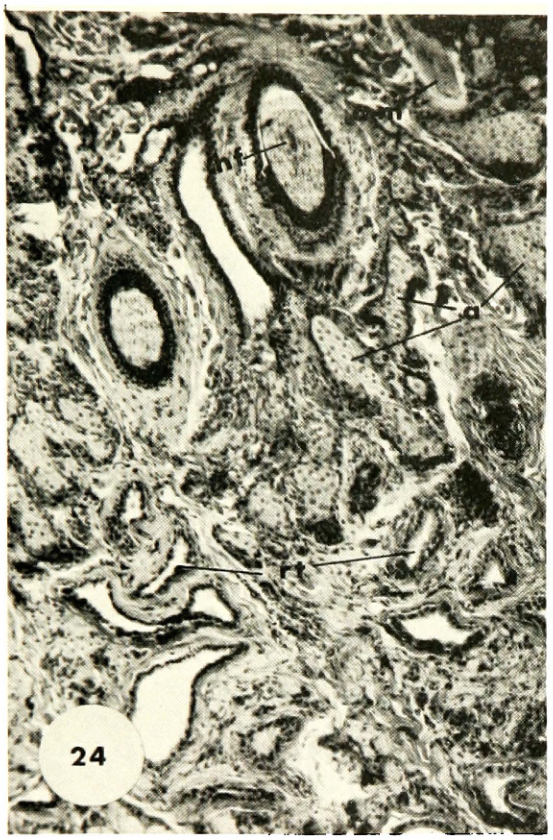
Explanation of Figures

Figure 24. Subauricular gland 69-1. Small undifferentiated sebaceous acini (a) are scattered around the hair follicles (hf). Arrector pili muscle (am), regressed apocrine tubules (rt). Approx. 84 X.

Figure 25. Subauricular gland 69-1. An undifferentiated sebaceous acini surrounded by numerous basal cells (bc). The central cells (cc) have small lipid vacuoles. Approx. 383 X.

Figure 26. Subauricular gland 69-1. An undifferentiated sebaceous acini is surrounded by dense connective tissue. Approx. 383 X.

Figure 27. Subauricular gland 69-1. Notice the minute lipid vacuoles in the central cells (cc), not the typical large lipid ~~vessicles~~ vacuoles of the active acini. Approx. 842 X.



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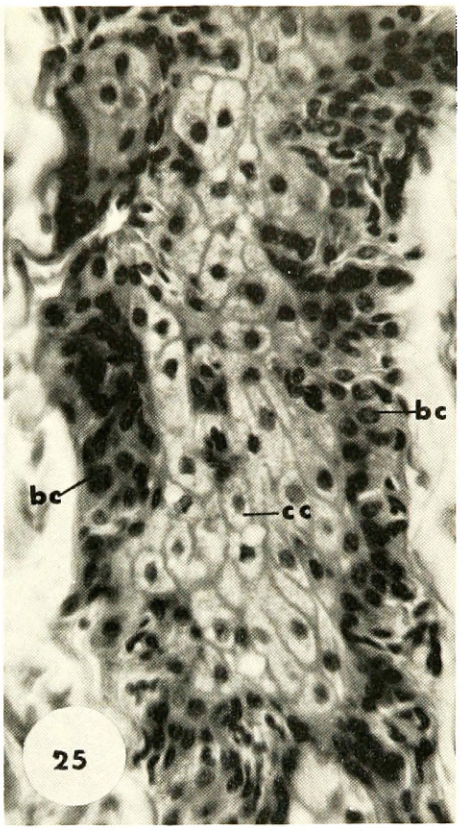

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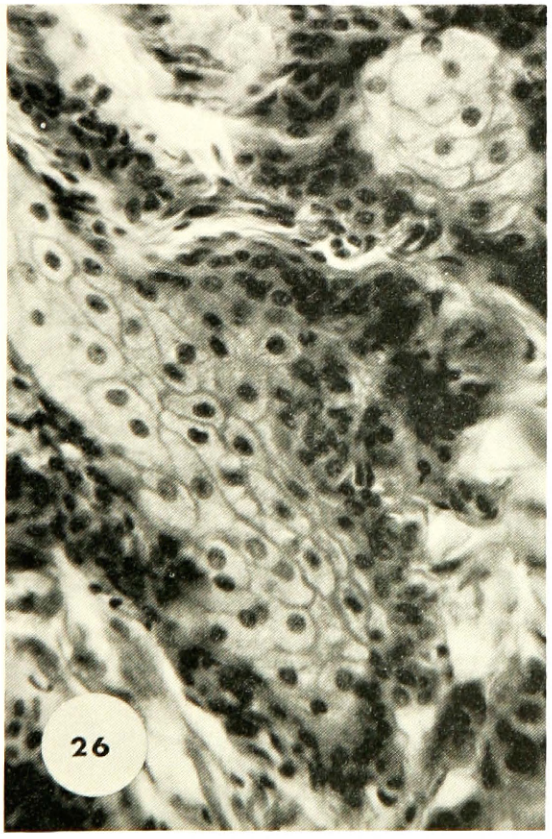

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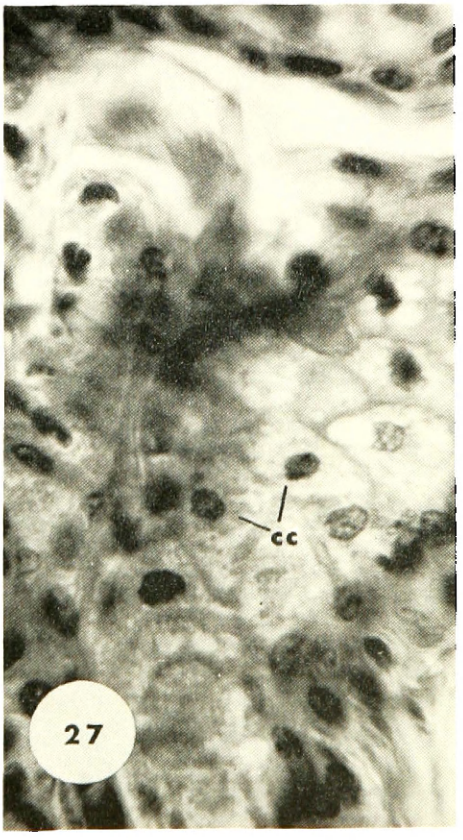

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Histochemistry of the Sebaceous Gland. The collagen of the connective tissue surrounding the acinus is colored green by aldehyde fuchsin, reddish-purple by Mallory Heidenhains, blue by Luxol fast, and pink by PAS. The perinuclear cytoplasm of the basal cells and the space around the lipid vacuoles of mature cells are stippled with fine dark granules by iron hematoxylin and toluene. Montagna (1962) described similar granules as mitochondria. The aldehyde fuchsin stain combines with mitochondria to demonstrate purple granules in the perinuclear space. Montagna (1962) mentioned that these granules may play a directive role in the synthesis of sebaceous lipids. The nuclear membrane, nuclear material and granules, shown by toluene and iron hematoxylin, vanish as cytolysis progresses in central cells. Faint evidence of acid mucopolysaccharides granules can be observed in the nuclei of basal cells, but the granules gradually disappear as the cells differentiate. The most peripheral cells of the acini contain minute perinuclear sudanophilic lipid bodies. As the cells mature, the sudanophilic gradules gradually enlarge. The lipid droplets in the mature acinus are spherical and uniform in size (Figure 11). Oil Red O is less sudanophilic in the basal cells.

Histology of the Apocrine Zone. The apocrine sudoriferous glands were first described by Horner in 1846 and later by Schiefferdecker in 1922. Since then, apocrine glands have received considerable attention. The sudoriferous

glands of two artiodactyls, the caribou and whitetail, have been described (Quay, 1952 and 1955). Apocrine glands develop from the follicular epithelium of the hair as do sebaceous glands (Montagna, 1962). According to Montagna (1967), apocrine glands take an intermediate position between "true secretion (or merocrine) and holocrine."

During the summer the apocrine zone consists of actively secreting coiled tubules of considerable length and diameter. These glands gradually regress to a quiescent state in December, but commence proliferation in February. The cyclic changes for the apocrine and sebaceous glands closely correspond (Figures 85 and 87). The greatest thickness of the apocrine zone is reached in June (5.33 mm.) and regresses to a low (0.85 mm.) in December (Table V).

The epithelium of the coiled tubules usually consists of one layer of cells that varies from a low cubodial to a columnar. One and sometimes two large spherical nuclei, measuring 5-9 μ in diameter, are located in the basal parts of the cell. The glandular units are surrounded by loose connective tissue and a few blood vessels. The terminal or apical portion of the secretory cell buds into the lumen. Fragments of the cytoplasmic protrusions obviously are fragmenting into the lumen. The columnar epithelium usually has a brush border, composed of micro villi and a cuticle. The tubules are surrounded by parallel spindle-shaped myoepithelian cells with elongated nuclei. The nuclei

measure 8-15 μ in length and 2-3 μ in width. These cells are tangential to the tubes and rest upon a thick, distinct hyalin basement lamina.

During the summer, numerous irregular clumps of apocrine cells without lumens are located between the tubules (Figures 29 to 31). These associated apocrine cell clumps have not been reported in the literature that I reviewed. The associated cells may either be cells of apocrine tubules that have not yet developed a lumen, or cells that somehow influence the secretory cells of the tubules. The associated apocrine cells differ from the secretory cells in that the basement membrane is thin and sometimes absent, and the myoepithelial cells are scarce; the cells are in very irregular clumps; and the cyclic activity and cellular details do not correspond with those of the secretory cells.

The apocrine secretory tubules become abruptly attenuated and emerge into a thin duct composed of one and sometimes two layers of cuboidal epithelium (Figure 42). This excretory duct is similar to what Quay (1955) reported for the tarsal gland of the caribou except that it is larger and is usually lined by one layer of cuboidal epithelium and not two layers of squamous epithelium (Figures 46 and 47). The duct has approximately a 10 μ lumen and a 30-35 μ outside diameter. It passes between the sebaceous acini and lies parallel to the hair follicles (Figures 42 and 43). As the duct approaches the hair orifice, it

becomes funnel-shaped and measures 50 μ near the opening (Figures 44 and 45). The terminal duct is composed of stratified squamous cells and empties into the pilosebaceous canal near the hair orifice.

Proliferation, Secretory Process, and Regression of the Apocrine Gland. In February, abrupt proliferation of the coiled tubules enlarges the apocrine gland, and the appearance of numerous clumps of apparently ductless associated apocrine cells are evident (Figures 29 to 31). By May, the ducts and lumens of the apocrine are large. The epithelium of the tubules change from a cuboidal to a columnar type which has a well-defined cuticular and brush border. The well-developed associated apocrine cells fill the space between the secretory tubules (Figures 31 to 33), but the associated cells, which are located at the basal part of the apocrine zone, are smaller and more elongated. They appear to be proliferating downward into the lower dense connective zone. These irregularly arranged clumps of associated cells have large spherical nuclei.

Some cytoplasmic buds and fragments are in the lumen of the gland during the spring months. The apical cytoplasm squeezes or oozes between the villi of the cuticular border, forming small beads on the surface that gradually grow in size until they begin to fragment or are pinched off (Figures 31 to 33). However, in June, most of the secretory cells reveal cytoplasmic extensions and

disappearance of the cuticular borders (Figure 34). The associated cells decrease in size and the nuclear membranes are distorted. This suggests that they have begun to atrophy. This drastic change may be related to the abrupt change in the secretory apocrine epithelium.

Little myoepithelial contraction is noticeable in July and August. The associated cells have regained their well-developed appearance except for a few scattered atrophied cells. A cuticular border begins to reappear in the secretory epithelium just distal to the nucleus, separating the newly made cuboidal cell from the large attached cytoplasmic extensions (Figures 35 to 37). The secretory epithelium now lies against the myoepithelial-basement membrane complex. A gradual breaking away of secretory material from the cytoplasmic extension occurs during the summer. The lumens of the gland are mostly filled with secretory material during August (Figure 35).

By September, the dialated tubules, composed of low cuboidal or squamous epithelium with small amounts of perinuclear cytoplasm, have exhausted their cytoplasmic extension supply (Figure 39). The nuclei of the secretory cells become smaller and the nuclear membranes are distorted. The reduced lumens of the gland are empty of secretory material. Some of the secretory cells begin to atrophy. Pkynotic cells are present in the lumens and excretory ducts (Figure 38). Denser connective tissue and numerous

fibroblasts invade the space between the coiled tubules.

From October to December the apocrine tubules and associated cells become progressively more atrophied and are continually being invaded by dense connective tissue and fibroblasts (Figures 40, 41, 48 and 49). By December, the quiescent apocrine zone is in its thinnest and most regressed stage (Figures 50 to 56). Many of the lumens of the coiled tubules are irregularly narrow or collapsed. Numerous pkynotic cells are sloughed into the lumens. Only a few unabsorbed atrophied associated cells are left imbedded in the connective stroma. In January some apocrine tubules are surrounded by a thick basement lamina which is the first evidence of regeneration in the regressed tubules. Also a few associated apocrine cells begin to appear among the tubules.

Histochemistry of the Apocrine Gland. The basement membrane surrounding the tubules is positive to PAS and stains dark pink. Fine cytoplasmic granules, large and fine nuclear granules, and the nuclear membrane are stained black with iron hematoxylin. Proteins are responsible for the precise staining action of iron hematoxylin. These granules seem to accumulate as the cells atrophy. Eosinophilic granules are scattered through the cytoplasm. They were previously demonstrated by Montagna (1962) and Quay (1955).

Aldehyde fuchsin stains the cytoplasm of the secretory and associated cells purple. Most of the fine purple granules are located at the basal portion of the secretory epithelium. Fine and large acid mucopolysaccharide granules are present in the nucleus and the cytoplasm of the secretory epithelium and apocrine associated cells. In the associated cells, the granules are scattered throughout, but in the secretory cells, they are congregated near the basal portion. As atrophy of the cells progresses, the basophilic granules, demonstrated with toluene, increase in number, even at the apex of the cell. No ferrous iron was demonstrated. The ferrous granules are also absent in other artiodactyls (Quay 1955) but have been reported in the human (Montagna, 1962). Perinuclear cytoplasm of the apocrine gland is filled with sparse sudanophilic droplets. More droplets accumulate in the taller secretory epithelium of the spring and summer glands. Oil Red O gives a weaker lipid reaction.

The Inner Zone. This zone is located directly below the apocrine zone and consists of dense connective tissue with abundant, parallel bundles of collagenous fibers. The lower portion of this zone is bordered by striated muscles. The thickness of this zone varies in individual animals but appears to be thickest during the summer months (Table V).

Blood Vessels. Numerous large blood vessels are located in the lower portion of the collagenous zone. Only

a few small arterioles and veins are present in the connective tissue between the apocrine and sebaceous zones, but the reticular zone is rich in small capillaries (Figures 30, 42 and 49).

Arrector Pili Muscles. The arrector pili muscles of the subauricular glands are very small, difficult to find, and do not always appear to be associated with each hair follicle (Figure 43). They are compact bundles of smooth muscle fibers which probably serve to force secretion from the sebaceous gland rather than for hair erection. This secretory method was mentioned by Quay (1955) for the arrector pili muscles of the caribou's tarsal gland. The muscle extends from the basal portion of the reticular zone to the connective tissue sheath near the basal part of the hair follice. The maximum diameter of the muscles is 0.05 mm.

The Hair Follicle. The small hair follicles are approximately 0.01 mm. in diameter and are more or less perpendicular to the surface of the gland. The hair follicles appear to penetrate the dermis more deeply during the summer (Table IV, Figure 43).

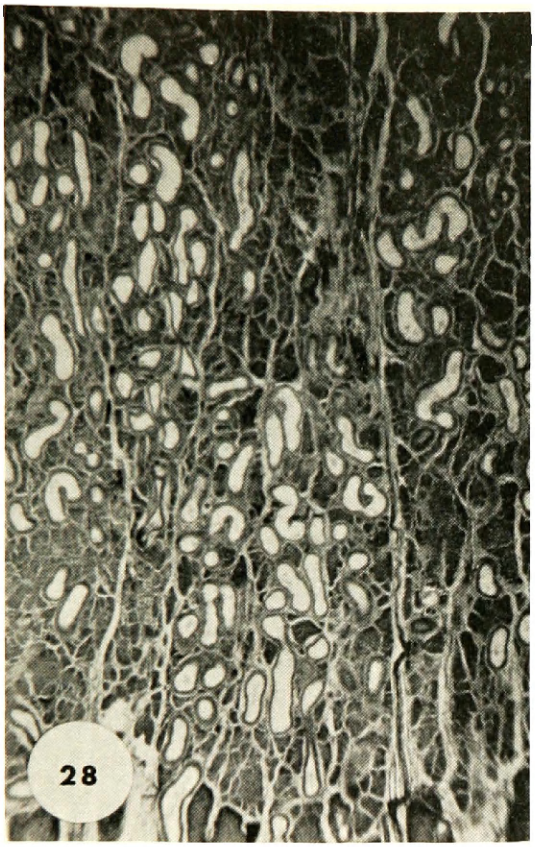
Explanation of Figures

Figure 28. Tubular arrangement of the apocrine zone of subauricular gland 62-3 from March. Approx. 34 X.

Figure 29. Subauricular gland 62-3. Thin secretory cells line the apocrine tubules (at). Small amounts of secretory material are present in the lumens. Irregular clumps of associated apocrine cells (aa) surround the tubules. Approx. 84 X.

Figure 30. Subauricular gland 62-3. Well-developed irregular clumps of associated apocrine cells (aa). Notice the arteriole (a). Approx. 383 X.

Figure 31. Tall columnar secretory cells (sc) line the May, 61-1 gland. Some cytoplasmic blebs are squeezed through the cuticular border (cb). Well-developed associated apocrine cells (aa), basement membrane (bm), myeopithelial nuclei (mn). Approx. 383 X.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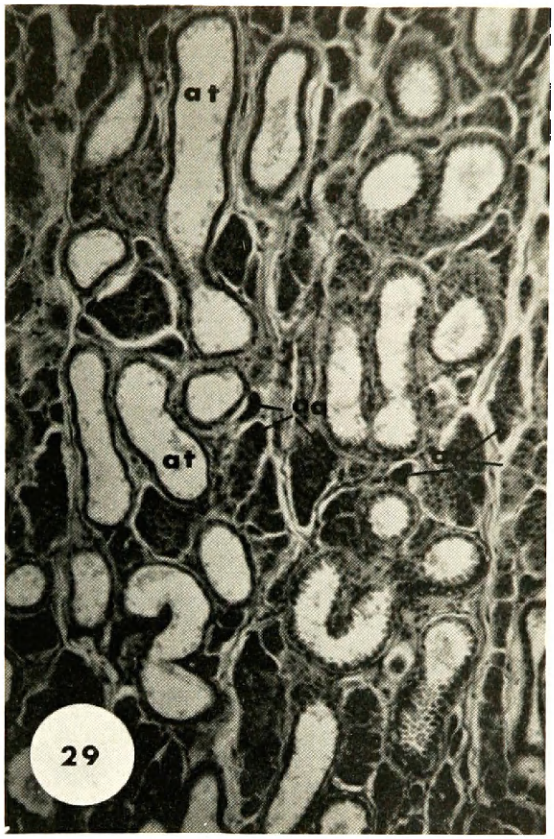

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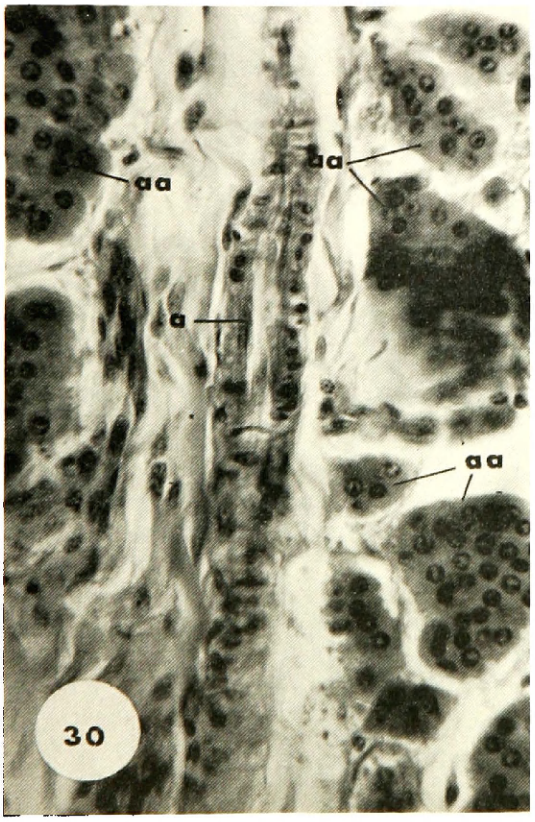

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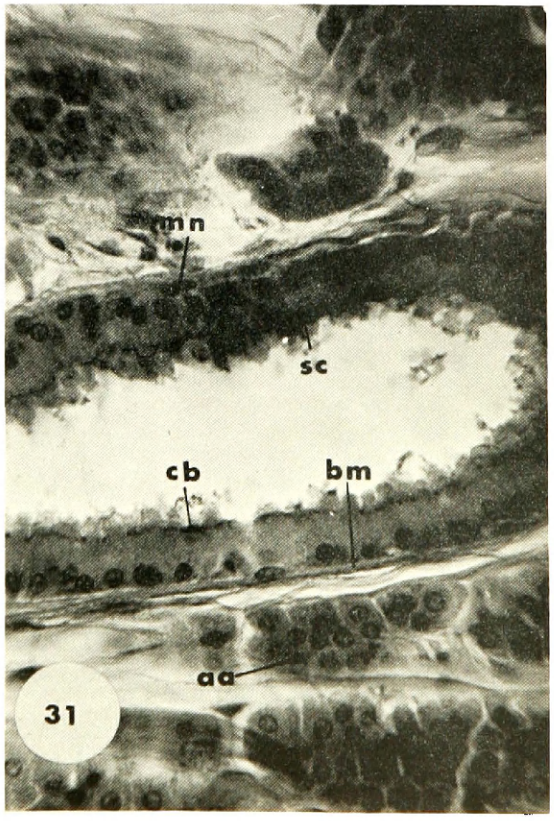

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Explanation of Figures

Figure 32. In May, subauricular gland 61-1, taller secretory cells line the tubules than were observed for March (Figure 29). Approx. 84 X.

Figure 33. Subauricular gland 61-1. The cytoplasmic blebs (b) squeeze through the cuticular border (cb) of the tall secretory cells. The blebs are pinched off or are fragmented (f) into the lumens. Approx. 842 X.

Figure 34. In June, subauricular gland 61-2, the distal cytoplasm is forced into the lumen by contraction of the epithelial cells. Cuticular border disappears. Lumens become filled with secretory material (sm). The associated apocrine cells appear slightly atrophied. Approx. 383 X.


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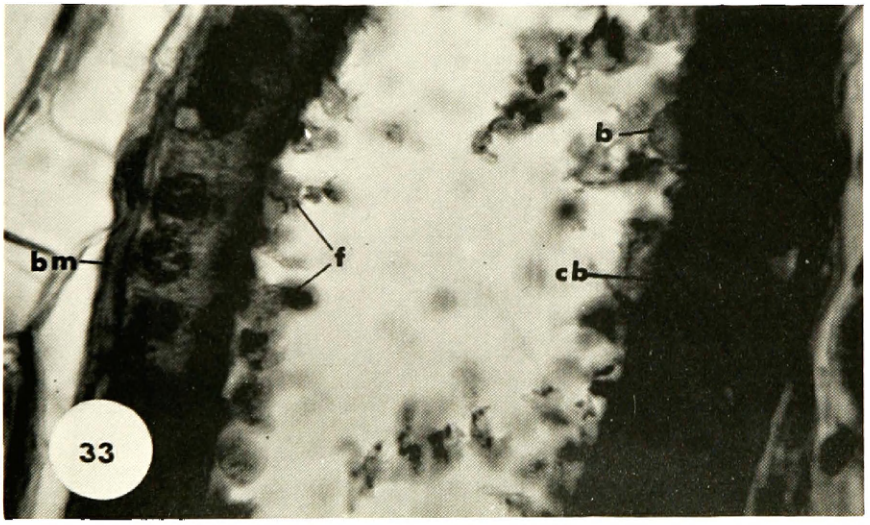
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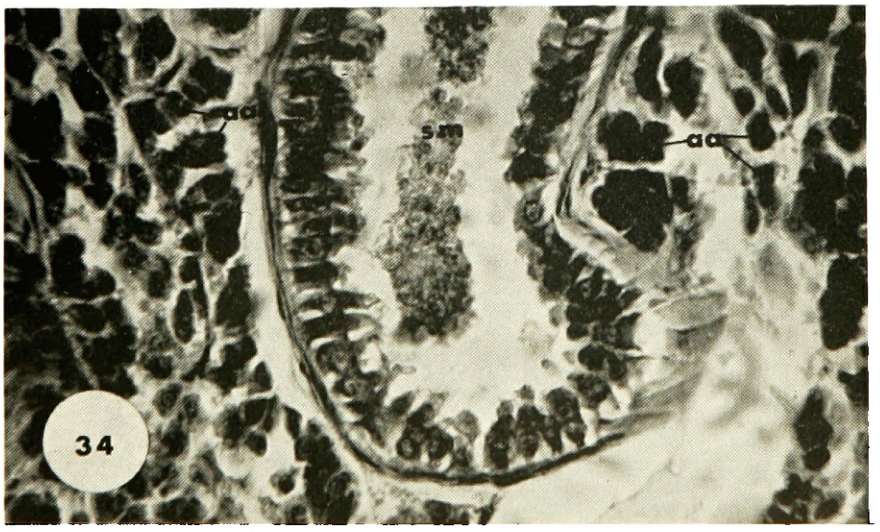
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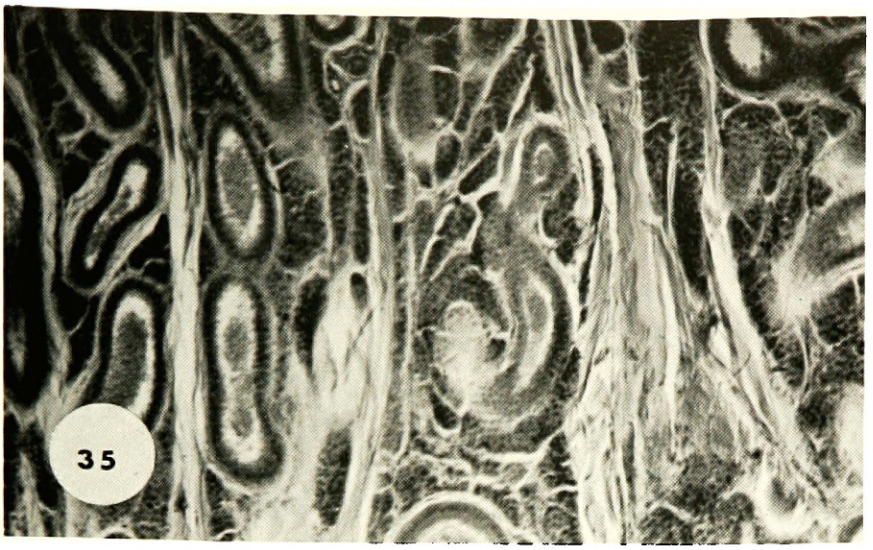
Explanation of Figures

Figure 35. In August, subauricular gland 61-4, the apocrine lumens are almost filled with secretory material. Approx 84 X.

Figure 36. Active secreting apocrine tubules of the August, subauricular gland 61-4. Approx. 383 X.

Figure 37. Subauricular gland 61-4. The cytoplasmic extensions (ce) are separated from the new cuboidal secretory epithelium (sc) by a reappearing cuticular border (cb). The associated apocrine cells (aa) appear developed. Approx. 842 X.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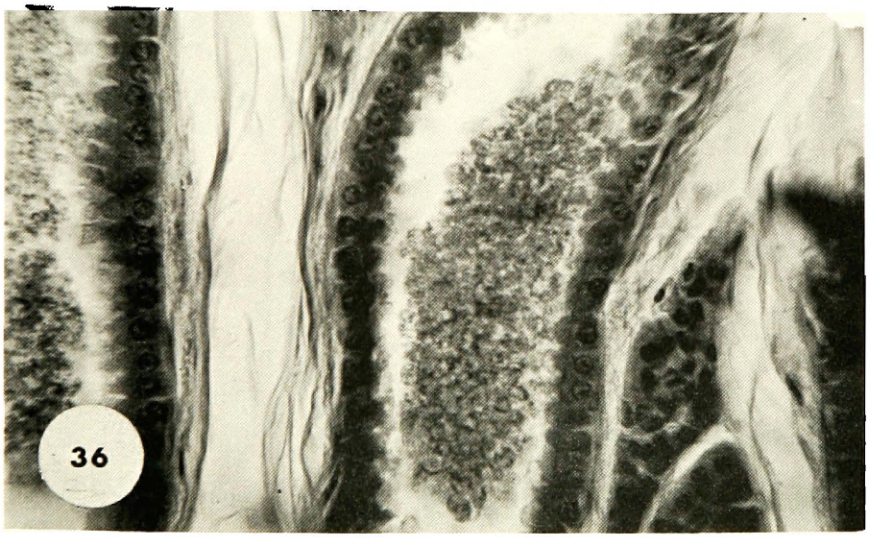
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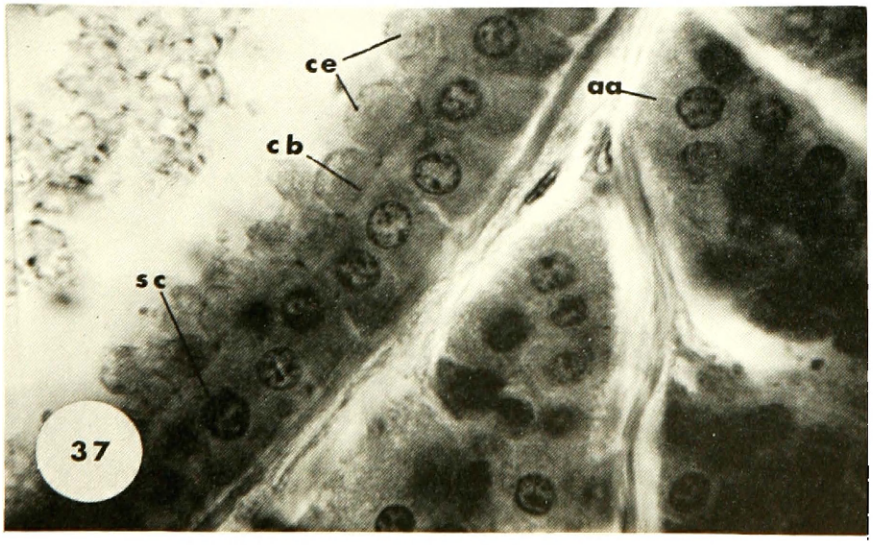
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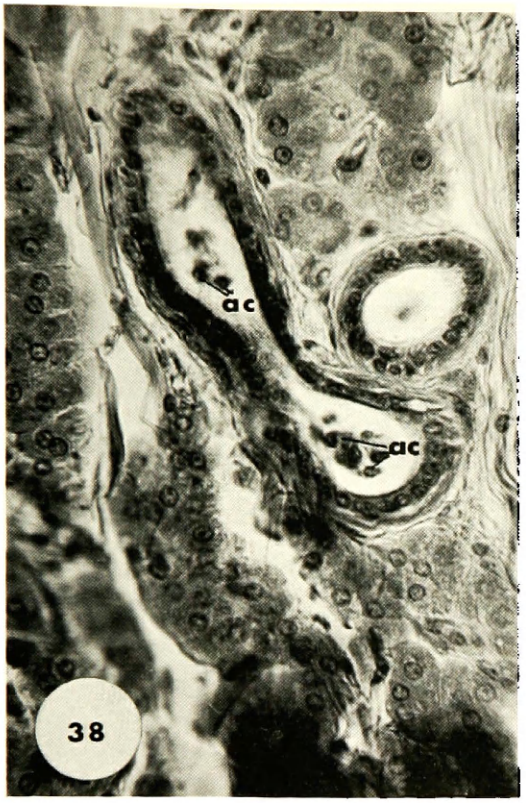
Explanation of Figures

Figure 38. Subauricular gland 61-5. The apocrine tubules beginning to atrophy. Notice the atrophied cells (ac) in the lumen. Approx. 383 X.

Figure 39. In September, subauricular gland 61-5, the low cuboidal cells (sc) of the tubules have exhausted their cytoplasmic extensions. Small irregular apocrine associated cells (aa) are located among the tubules. Approx. 383 X.

Figure 40. Subauricular gland 61-6. The associated apocrine cells (aa) have begun to atrophy and are being invaded by connective tissue (ct). Approx. 383 X.

Figure 41. Subauricular gland 61-6. The apocrine ducts and lumens have decreased in size. Slightly atrophied appearance of apocrine tubules and associated cells. Notice the large amounts of denser connective tissue forming around the tubules and the fewer associated apocrine cells (aa). Approx. 383 X.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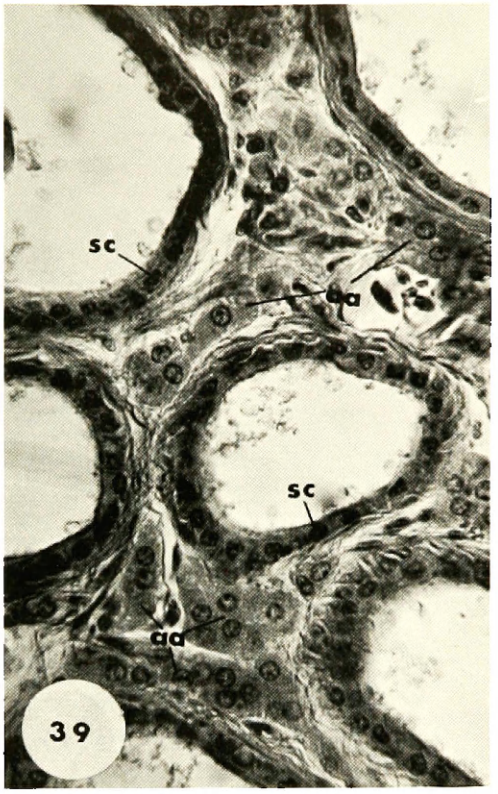
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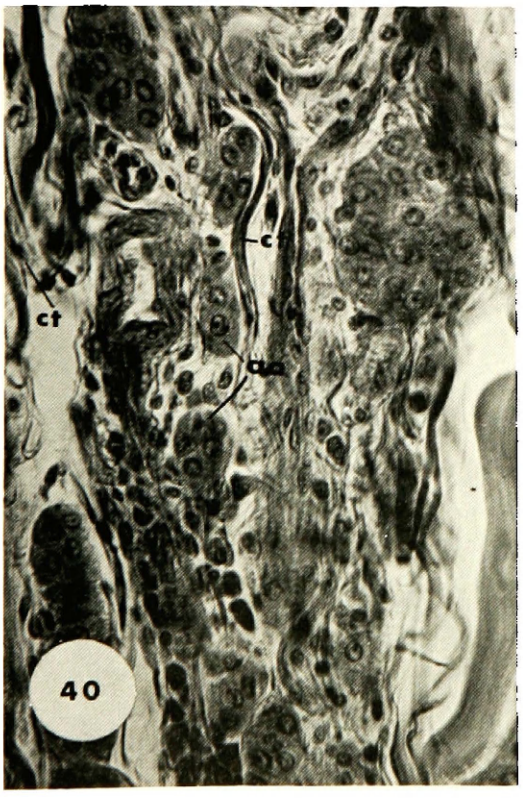
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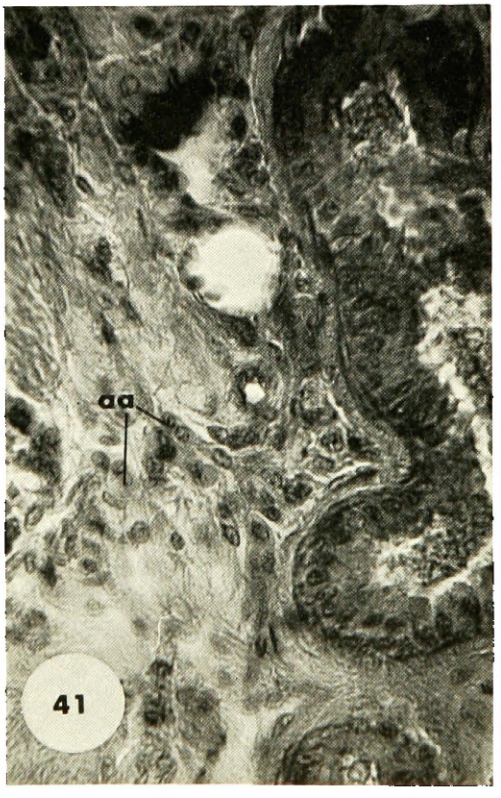
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Explanation of Figures

Figure 42. Subauricular gland 62-3. The apocrine secretory duct emerges into the excretory duct (1) and passes between the sebaceous acini (2). Arteriole (a). Approx. 84 X.

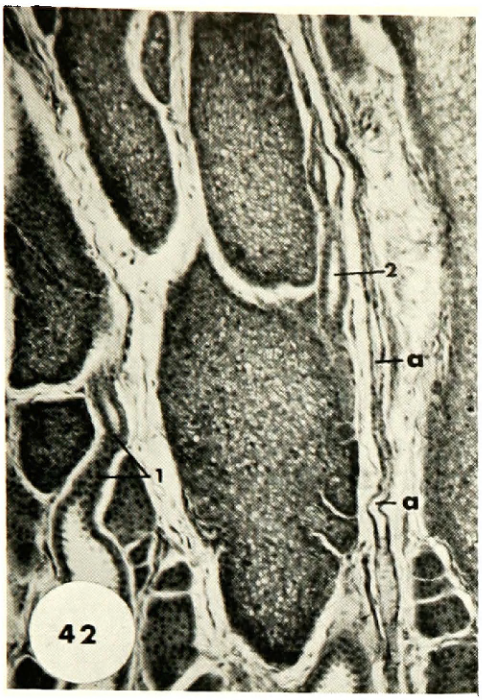
Figure 43. Subauricular gland 62-3. The thin excretory duct (ed) parallels the hair follicle (hf). Arrector pili muscle (am). Approx. 84 X.

Figure 44. Subauricular gland 62-3. The funnel-shaped excretory duct (ed) empties into the pilosebaceous canal near the hair orifice (ho). Approx. 84 X.

Figure 45. Subauricular gland 62-3. The funnel of the excretory duct (ed) is composed of multi-layers of stratified squamous epithelium. Approx. 383 X.

Figure 46. Subauricular 61-1. Notice the thin walls of the excretory duct. Approx. 383 X.

Figure 47. The excretory duct of gland 61-5 from September is filled with atrophied secretory cells (ac). Approx. 383 X.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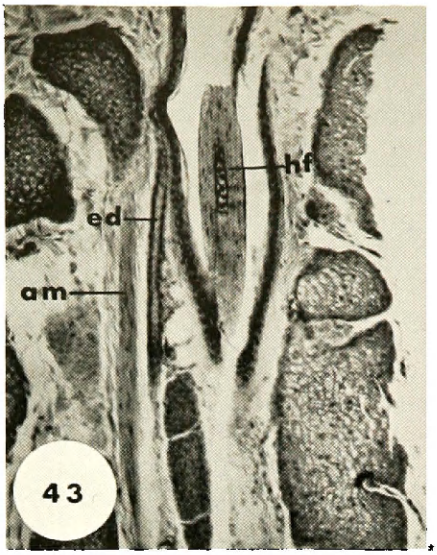
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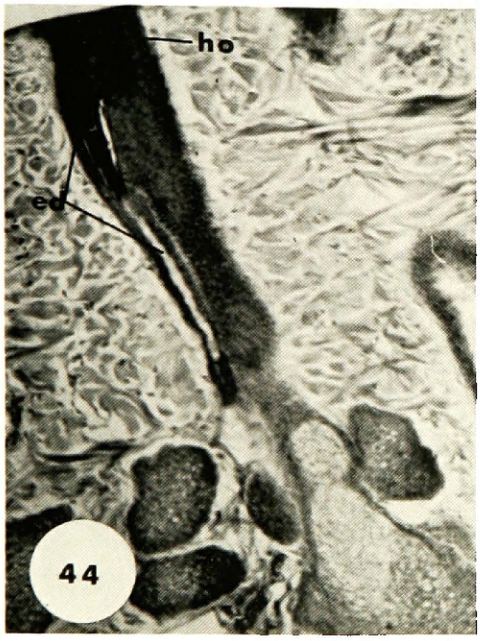
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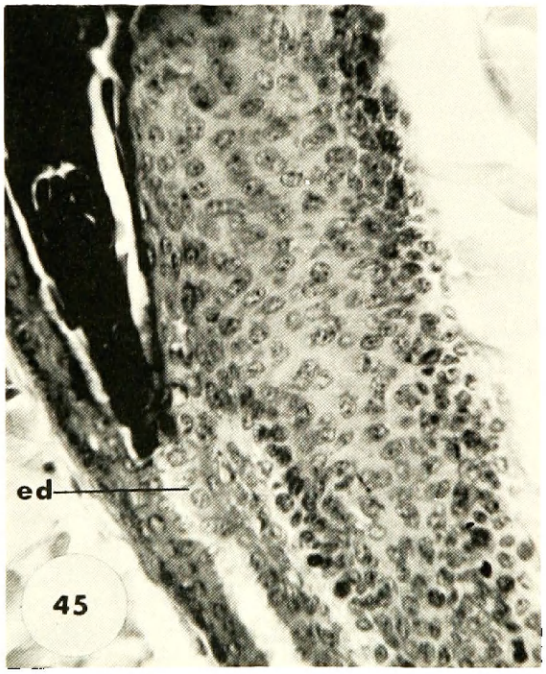
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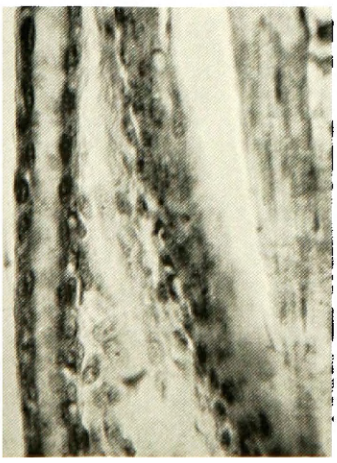

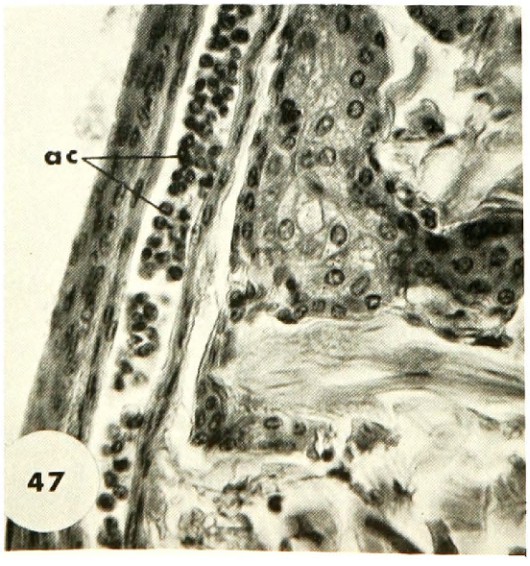
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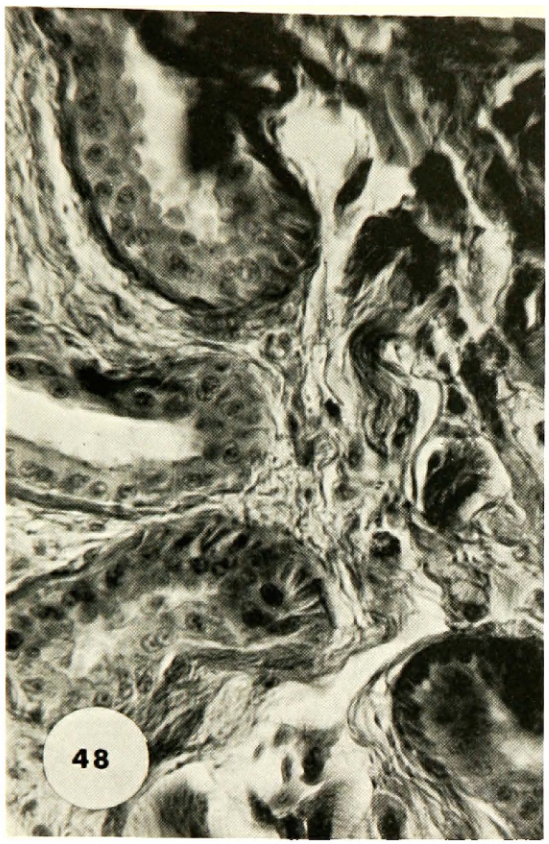
Explanation of Figures

Figure 48. Subauricular gland 61-7. Only dense tissue surrounds the regressed apocrine tubules. No associated apocrine cells are present. Approx. 383 X.

Figure 49. Subauricular gland 61-7. The secretory cells are undergoing atrophy. Little secretory material is present in the lumens. Arteriole (a). Approx. 383 X.

Figure 50. Subauricular gland 61-8. The apocrine tubule (1) is atrophied. Secretory cells are being sloughed into the lumen (2). Notice the dense connective tissue. Approx. 383 X.

Figure 51. Subauricular gland 61-8. A partially atrophied tubule (at). The atrophied secretory cells are being sloughed. Approx. 842 X.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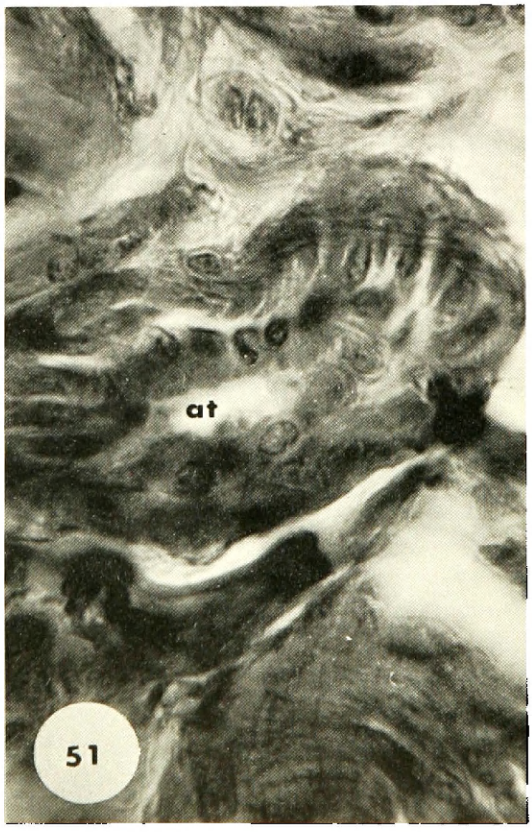
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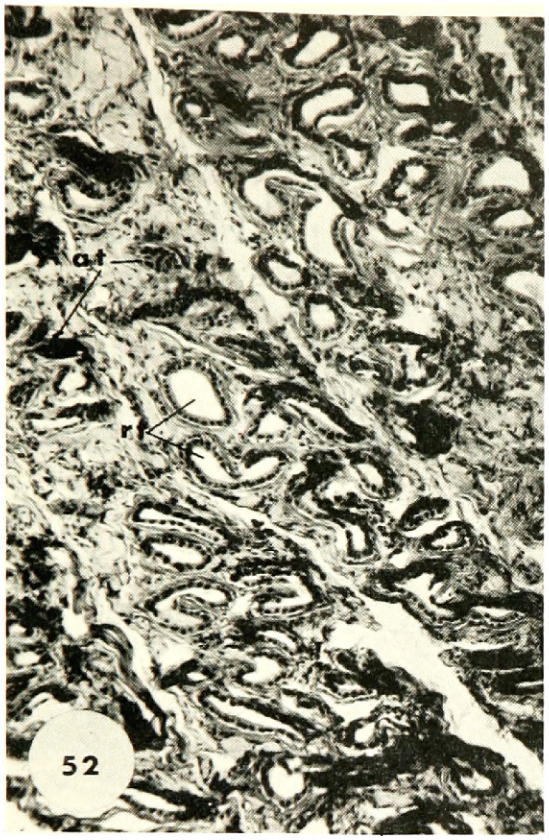
Explanation of Figures

Figure 52. The apocrine zone of the January subauricular gland, 69-1. Notice the atrophied apocrine tubules (at). The regressed tubules (rt) have begun to regenerate. Approx. 84 X.

Figure 53. 54. The atrophied apocrine tubules of subauricular gland 69-1. Approx. 383 X.

Figure 55. Subauricular gland 69-1. Apocrine tubules are surrounded by a thick basement membrane (bm), which is first evidence of regeneration in the regressed tubules. Notice the thin cells lining the tubules. Approx. 383 X.

Figure 56. A few associated apocrine cells (aa) have begun to appear among the tubules in the January 69-1 gland. Approx. 383 X.



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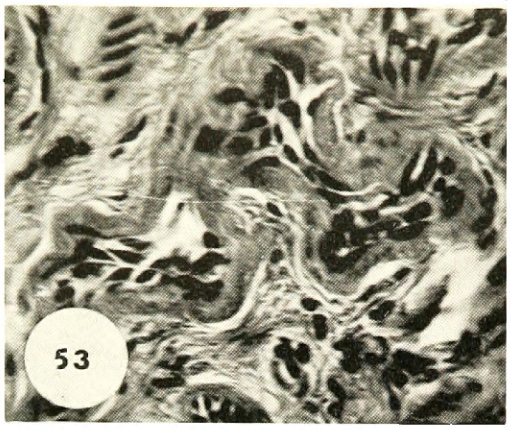

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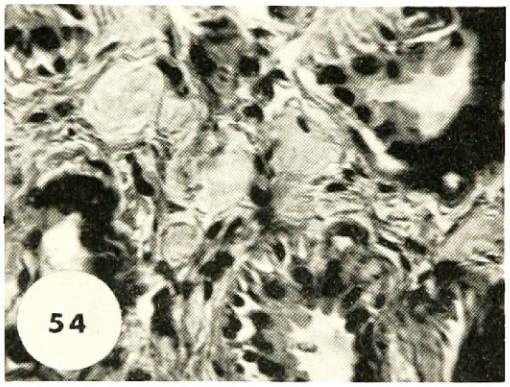

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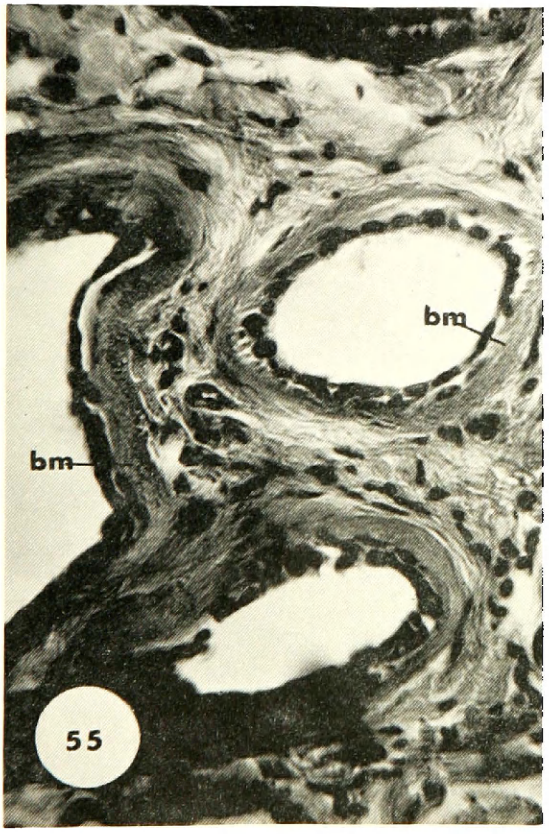

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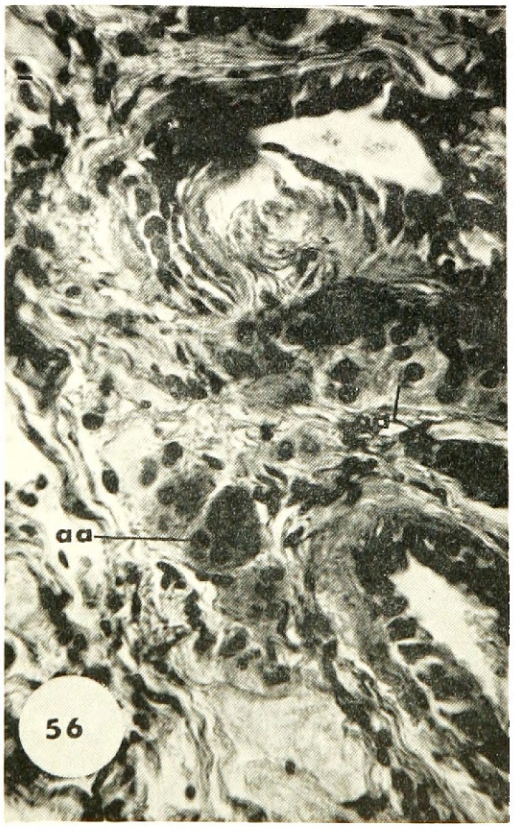

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Rump Gland

Gross Description. The paired rump glands are located in a thickened area of skin in the center of the white rump patch of both sexes (Figures 57 and 58). Unfortunately, some of the material available for sectioning had been poorly fixed. These were glands 62-3 for March, 63-4 for April, 61-4 for August, and 61-6 for October. The rump glands from the castrated animals are included in this portion of the results because they were similar to glands from normal animals.

The shape of the rump gland is circular (Figure 59). The diameters range from 19.5-43.3 mm. (Table VII). The center of the gland has the greatest glandular development. The gross glandular measurements presented in Table VII reveal no significant seasonal variation. The one female rump gland is slightly thicker than in the males; otherwise no other sexual distinctions could be made.

The hairs of the rump gland and the rump patch are white and are significantly larger (approximate length of 50-70 mm. and a diameter of 0.35-0.52 mm.) than those of the subauricular gland, but are slightly smaller than the adjacent hairs (approximate length of 65-80 mm. and a diameter of 0.45-0.55 mm.). All the hairs of the gland pass diagonally into the dermis at approximately 60 degrees (Figure 59). Tannish secretory material is usually adhering to the hairs (Figures 58 and 59).

TABLE VII

Gross Measurements of the Rump Gland

Month and Specimen No.		Diameter of gland in mm.	Maximum skin-gland height in mm.	Maximum gland thickness in mm.
January	62-1	27.0	3.9	2.7
January	69-1	31.6	4.8	2.7
February	68-2	19.5	4.2	3.0
March	62-3	24.9	3.6	2.6
April	62-4	23.4	4.2	3.4
May	61-1	27.8	4.9	3.4
June	61-2	27.7	4.7	4.2
July	61-3	31.0	5.2	4.2
August	61-4	--*	3.7	2.1
September	61-5	35.4	4.5	2.9
October	61-6	25.8	4.6	3.8
November	61-7	34.5	5.4	4.2
December	61-8	24.0	5.1	4.3
Female Rump Gland				
October	68-10	25.9	6.5	4.7
Rump Gland of Castrates				
August	H3561	--*	6.9	4.4
August	H3089	43.3	4.7	2.7
August	H3082	32.6	6.0	5.3

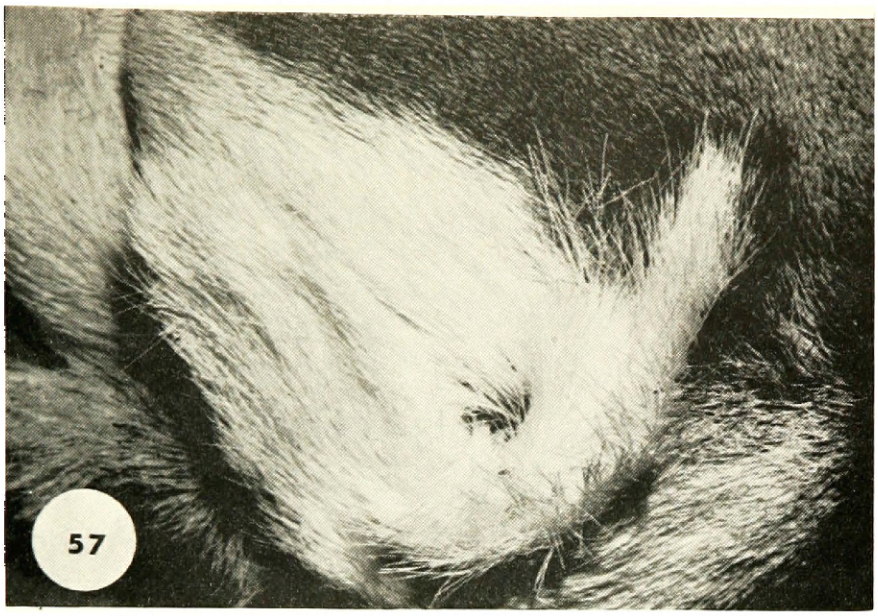
*Some of the glands were not dissected entirely and their measurements were omitted.

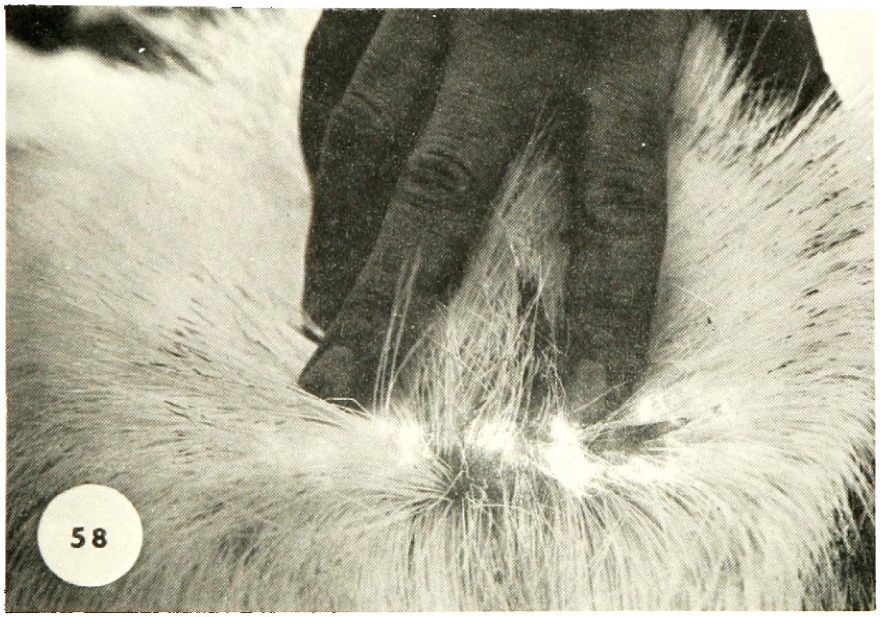
Explanation of Figures

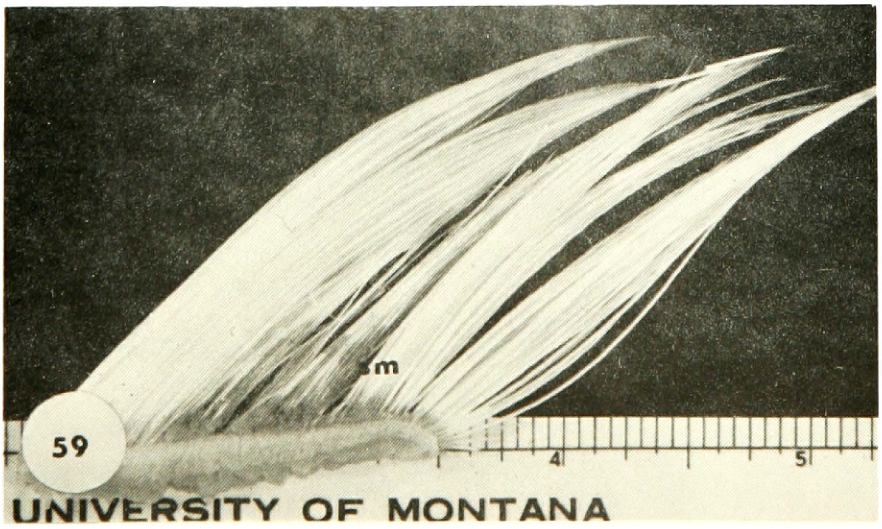
Figure 57. Rump gland 69-1. The rump gland is located in the middle of each rump patch. The dark glandular secretions mark the location.

Figure 58. Rump gland 69-1. The dark secretory material clings to the hairs.

Figure 59. Rump gland 69-1. The rump hairs are diagonal to the gland's surface. Notice the secretory material (sm). The gland is circular and has a maximum glandular thickness at the center. Approx. 9/8 X.







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The surface of the gland is covered by numerous ridges and folds. Directly beneath the gland, there is usually a thin layer of a dense collagenous tissue, not the thick layer that is characteristic of the remaining rump patch.

Glandular Components. The rump gland is divisible into essentially the same areas as the subauricular gland; the epidermis and the four zones of the dermis (outer zone, sebaceous, apocrine, and a inner zone) (Figure 60).

Epidermis. The epidermis of the rump gland is relatively thick ranging from 30-110 μ and 2-7 nucleated cells deep (Table VIII). The thickest portion is the stratum disjunctum and the stratum corneum which measures to a maximum of 80 μ between the surface folds and ridges and around the orifice of the hair follicles. The underlying stratum granulosum is composed of one and sometimes two layers of squamous cells with elongated nuclei measuring 8-15 μ in length. The deepest layer, the stratum germinativum, ranges from 10-60 μ in thickness and shows monthly variations. The polyhedral cells and ovoid basal cells of this layer are similar to those of the subauricular gland. Only a few pigmented granules are located in the epidermis.

Outer Zone. The papillary layer of the rump gland is thinner and consists of denser connective tissue than in the subauricular gland. Also, the underlying reticular layer is relatively thin and quite constant in depth. Approximate

TABLE VIII

Measurements of the Epidermis of the Rump Gland at 1000 X

Month and Sample No.		Range of the epidermis thickness μ	Number of cells thick in the epidermis
January	62-1	20-50	3-5
January	69-1	30-70	3-5
February	68-2	30-70	3-5
May	61-1	20-65	2-7
June	61-2	19-80	2-6
July	61-3	20-60	3-5
September	61-5	45-105	3-9
November	61-7	30-75	2-7
December	61-8	25-70	3-7
Female Rump Gland			
October	68-10	30-110	3-5
Rump Gland of Castrates			
August	H3561	15-70	3-5
August	H3089	25-80	3-7
August	H3082	20-60	3-8

range in thickness of the reticular layer of the rump gland is 0.30-0.50 mm. (Table IX). This layer is composed of parallel collagenous bundles with numerous fibroblasts and elastic tissue.

Histology of the Sebaceous Zone. Beneath the reticular zone are the small lobulated sebaceous glands. Each gland lies next to and secretes into the side of the associated hair follicle. The sebaceous gland demonstrates no seasonal variation. The approximate range in zone height ranges from 0.55-0.90 mm. for the male glands. This zone in the female and castrates is slightly thicker, measuring 1.10 mm. and 0.93-1.20 mm., respectively (Table IX). Each acinus is encapsulated by a fibrillar connective tissue sheath with dense connective tissue between the widely spaced sebaceous units (Figure 65). The deminsions of the basal and central cells are similar to those of the sub-auricular gland.

The sebaceous glands from all the specimens reveal a low level of secretory activity. The central cells of the acini undergo slight differentiation and contain only minute lipid vacuoles (Figure 61). The acini nearest the hair follicle and excretory duct are slightly more developed. The nuclei of their central cells are in various stages of disintegration. Some of the excretory ducts from the different lobulated acini join into one large common duct (Figures 61 and 63) which empties into the pilosebaceous

TABLE IX

Approximate Measurements of the Dermis at 100 X in mm. and the Estimation of Apocrine Adipose Tissue of the Rump Gland

Month and Specimen No.	Reticular Zone	Sebaceous Zone	Apocrine Zone	Hair Follicle Depth	Estimation of of Adipose Tissue
Jan 62-1	.33	.65	2.1	---	+
Jan 69-1	.50	.80	1.8	2.9	+
Feb 68-2	.30	.55	1.2	1.5	+
May 61-1	.40	.70	1.8	1.5	+
Jun 61-2	.37	.70	1.7	2.1	+
Jul 61-3	.30	.72	1.9	2.5	++
Sept 61-5	.35	.65	2.0	1.5	+
Nov 61-7	.44	.90	1.9	2.4	+
Dec 61-8	.35	.85	1.8	2.6	+
Female Rump Gland					
Oct 68-10	.30	1.10	2.8	2.2	+++
Rump Glands of Castrates					
Aug H3561	.55	1.10	2.1	3.1	+++
Aug H3089	.35	.93	1.5	2.9	+++
Aug H3082	.50	1.20	1.8	3.2	+++

0 = no adipose tissue
+ = slight amount of adipose tissue
++ = moderate amounts of adipose tissue
+++ = considerable amounts of adipose tissue

canal. This duct measures 200 μ in a gland taken in September. It is lined with stratified squamous epithelium that is continuous with the walls of the pilosebaceous canal.

Secretory Process of the Sebaceous Gland. The rump gland differs from the subauricular in that it 1) has no large sebum storage vessicles or completely differentiated acini; 2) appears to be secreting at somewhat constant rate throughout the year; 3) reveals little change in the differentiating state of the acini; 4) accumulates only very minute lipid vacuoles within the cells.

Histochemistry of the Sebaceous Gland. The connective tissue encapsulating the acini are stained dark purple by Mallory Heidenhains, dark pink by PAS, and blue by Luxol fast blue. The epithelium of the blood vessels and the epidermis are colored purple by thionin. Sudan B stains the outer layers of the epidermis, the epidermal sheath around the hair follicle, and the pilosebaceous canal blue. The center of the mature acini and the excretory ducts are completely stained dark blue, but along the periphery of the acini, only small scattered sudanophilic droplets are observed. Oil Red O gives results similar to Sudan B except that it is less sudanophilic, especially along the periphery of the acini.

The perinuclear cytoplasm of the basal cells and the space around the lipid vacuoles of the more mature cells are stippled with fine, darkly stained granules, demonstrated

by iron hematoxylin. These granules disappear as the cells mature. Fine acid mucopolysaccharides granules, stained by thionin, are scattered through the undifferentiated cells.

Toluidine blue reacts differently with the various rump glands. Some glands take the stain while others take it lightly or not at all. The glands that do stain have both small and large nuclear and cytoplasmic granules in the basal cells. These cells gradually lose their granules as the cells mature. The nuclear membrane of some of these glands stain while others do not. The basal cells of a gland from January (69-1) reveals large positive PAS granules in the perinuclear cytoplasm but the gland from a castrated animal (H3561) has none. I cannot conclude whether differences in staining are significant or caused by faulty procedures or unstable stains.

Histology of the Apocrine Zone. The apocrine zone of the rump gland consists of coiled tubules of considerable size. The tubules are more coiled than those of the subauricular gland. The rump gland maintains its large dimensions throughout the year and there is no evidence of seasonal change as is so apparent in the subauricular gland (Figures 66 and 67).

The apocrine zone is relatively constant in height and ranges from 1.2-2.1 mm. for all male antelope. The zone of one female gland is slightly thicker and measures 2.8 mm., Table IX.

Explanation of Figures

Figure 60. A cross section of a January rump gland 69-1. Notice the arrangement of the apocrine tubules (at) and the lobulated sebaceous acini (sa). Epidermis (e). Approx. 34 X.

Figure 61. Rump gland 61-8. The slightly differentiated lobulated acini empty into a common excretory duct (ed) that empties into the pilosebaceous canal (pc) along the hair follicle. Arrector pili muscle (am), apocrine excretory duct (ad). Approx. 84 X.

Figure 62. Rump gland 68-10. The arrector pili muscle (am) along the hair follicle (hf) is large. Approx. 84 X.

Figure 63. Rump gland 68-10. Lobular arrangement of the sebaceous acini and the common excretory duct (ed). Notice the apocrine excretory duct (ad) winding among the sebaceous acini. Approx. 84 X.

Figure 64. Rump gland 61-5. The hair follicles (hf) are surrounded by sebaceous acini and large arrector pili muscles (am). Approx. 84 X.

Figure 65. Rump gland 69-1. Dense connective tissue (ct) fills the interlobular space between the sebaceous units. Apocrine tubular (at). Approx. 84 X.


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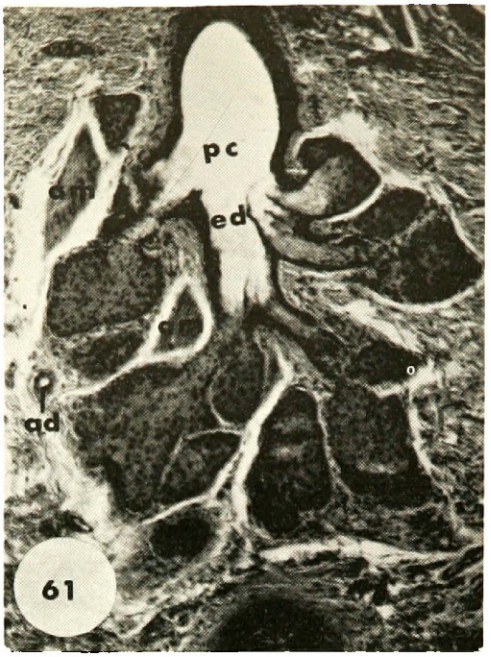
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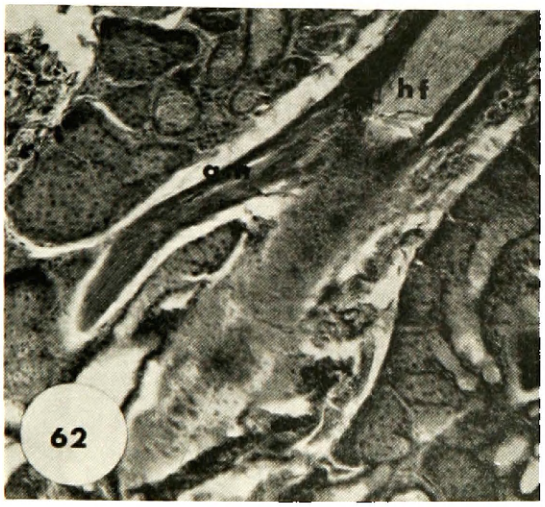
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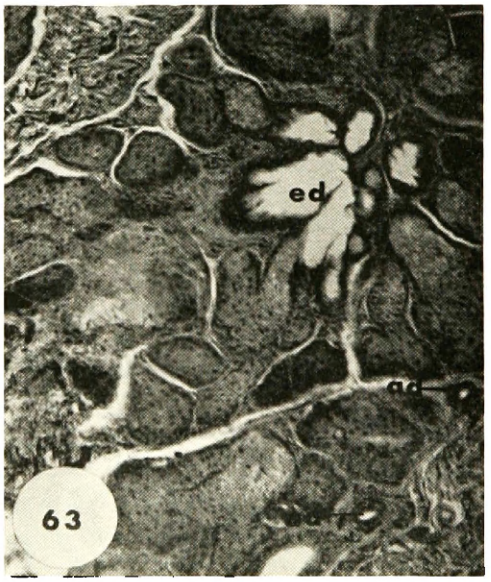
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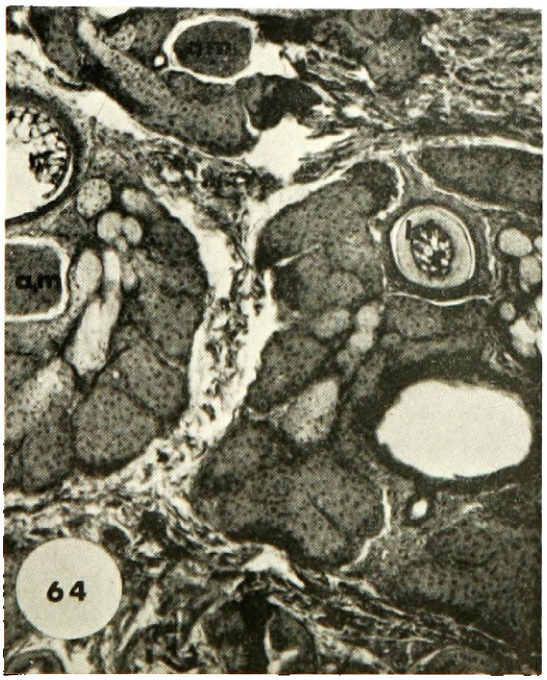
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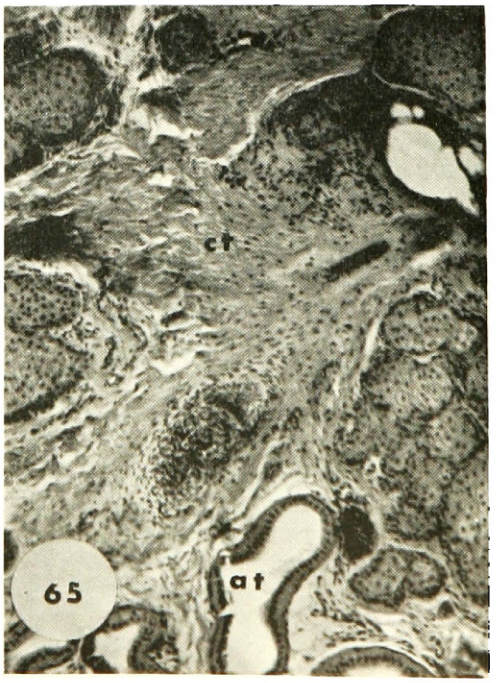
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Columnar secretory cells line the large tubules (Figure 68). One and sometimes two large spherical nuclei, 5-8 μ in diameter, are located near the center of each secretory cell. The terminal portion of the secretory cells has a cuticular border but no brush border. No clumps of associated apocrine cells common for the sub-auricular gland are present among the tubules. Spindle-shaped myoepithelial cells, with elongated nuclei measuring 9-17 μ in length and 2-4 μ in diameter, lie on the inner portion of the thick basement membrane that sheaths the tubules (Figure 71). The inter-tubular space is filled with very loose connective tissue, numerous blood vessels and adipose tissue (Figures 66 and 67). Adipose tissue is more evident during the summer months when the antelope characteristically add fat to their bodies (Table IX).

The apocrine tubules narrow to form the excretory ducts, which are lined with a single layer of cuboidal cells but emerge into a double layer as the duct approaches the hair follicle (Figure 76). The duct winds through and around the sebaceous acini on the underside of the hair follicle, and empties into the pilosebaceous canal near the hair orifice. The lower protion of the duct is approximately 25 μ outer diameter. Near the hair orifice the duct enlarges into a funnel (Figure 77), and is lined by several layers of cells that are continuous with epithelium that sheaths the hair follicle. The funnel opening has an

approximate outer diameter of 60 μ and a lumen diameter of 20 μ.

Secretory Process and Evidence of Regression in the Apocrine Gland. The apocrine portion of the rump gland produces a slight amount of secretion throughout the year, and no one gland secretes noticeably more than others. Only small amounts of secretory material are present in the apocrine lumens.

In the process of secretion, the apical cytoplasm is squeezed or oozed through the cuticular border to form small secretory buds which fragment or pinch off into the lumen.

Atrophy was observed in only one long apocrine tubule of the female rump gland (Figures 72 to 74). The lumen of this tubule is partially or completely collapsed and the cells and nuclei are darkly stained. Many of the cell membranes appear to have disintegrated.

Histochemistry of the Apocrine Gland. The histochemistry of the basement membrane and connective tissue is the same as in the subauricular gland and the sebaceous portions of the rump gland. The cytoplasm of the secretory cells of a gland from January 69-1 has numerous PAS positive granules but only very fine cytoplasmic granules in a gland from a castrate (H3561). Fine acid mucopolysaccharide granules, eosinophilic granules, and granules stained by iron hemotoxylin are present in the cytoplasm of all rump

glands. Toluidine blue demonstrates cytoplasmic and nuclear granules and stains the nuclear membranes of some glands. Some acid mucopolysaccharide granules in the nuclei of the secretory cells are demonstrable with thionin. Large sudanophilic droplets are situated around some of the tubules. Considerably more granules are found in the rump gland than were noted for the subauricular glands. The apical portion of the secretory epithelium appears slightly more sudanophilic. Oil Red O gives similar results but is less sudanophilic.

The Inner Zone. The inner zone is located directly beneath the apocrine zones, and is relatively thin, ranging from 0.30 to 0.90 mm. The thick dense collagenous layer that is characteristic of the rump patch is thin or absent in the area beneath the gland. The tissue of this zone varies from a delicate connective tissue, filled with numerous adipose droplets (Figure 67), to a denser connective stroma of collagenous fibers, oriented in parallel wavy bundles, with a few adipose droplets among them (Figure 75). The histology of this zone is considerably different than that which was described for the subauricular gland.

The Blood Vessels. The rump gland is richly supplied throughout with blood vessles. It is considerably more vascularized than the subauricular gland. The larger arterioles are frequently located in the inner zone (Figure 67). Many capillaries are in contact with the basement

lamina of the apocrine tubules, around sebaceous acini and in the reticular zone (Figures 69 and 70).

Arrector Pili Muscles. The arrector pili muscles of the rump gland are large and are associated with each hair follicle (Figures 62 and 64). These compact bundles of smooth muscle fibers undoubtedly serve to force secretion from the sebaceous gland as well as for hair erection. The muscle extends from the connective tissue at the base of the hair follicle to an area immediately beneath the epidermis. The maximum belly diameter and length of the muscles are 0.15 mm. and 1.50 mm. respectively.

The Hair Follicle. The hair follicles are diagonal to the epidermal surface and penetrate deeply into the apocrine zone (Figure 75). The maximum diameter of the hair follicle is 0.32 mm. The various maximum lengths of the hair follicle for each gland are recorded in Table IX. Few small hairs are present. They measure 20-30 μ in diameter and have a maximum length of approximately 0.50 mm.

Explanation of Figures

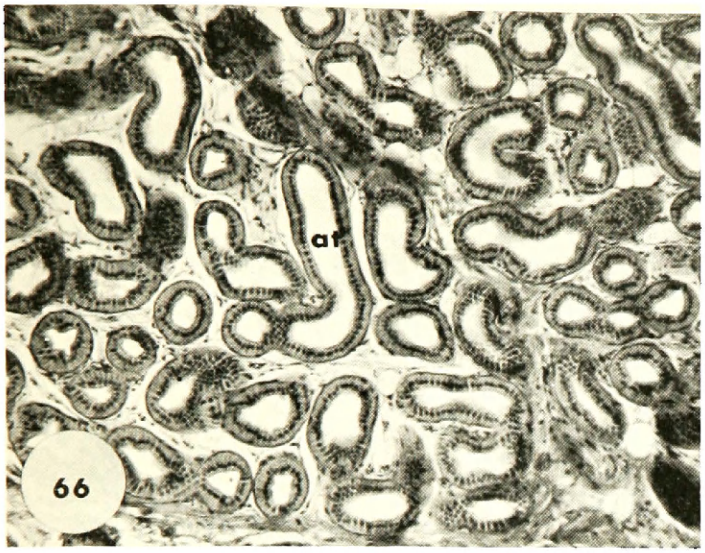
Figure 66. The apocrine tubules (at) of a January rump gland 69-1. Notice the large size of the tubules and secretory epithelium, and the small amounts of secretory material in the lumens. Approx. 84 X.

Figure 67. The apocrine tubules (at) of an August rump gland H3561 from a castrated animal. Notice the large amounts of adipose tissue (adt) surrounding the tubules. This is typical of the glands from the summer months. The apocrine tubules are not as concentrated as those from January represented in Figure 66. An artery (a) is found in the connective and adipose tissues of the inner zone. Approx. 84 X.

Figure 68. Rump gland 61-2. Note the tall secretory cells (sc) that are characteristic of the rump glands. The secretory process of the tubules was minimal in all rump glands examined. Cuticular border (cb). Arteriole (a) is among the tubules. Approx. 383 X.

Figure 69. 70. Rump gland 61-1 and 61-2. The apocrine zone is richly supplied with capillaries (c) and arterioles (a) respectively. Approx. 383 X.

Figure 71. Rump gland 61-1. Note the thick basement membrane surrounding the apocrine tubules. Myoepithelial nuclei (mn), basement membrane (bm). A small capillary (c) is located in the connective tissue between the tubules. Approx. 842 X.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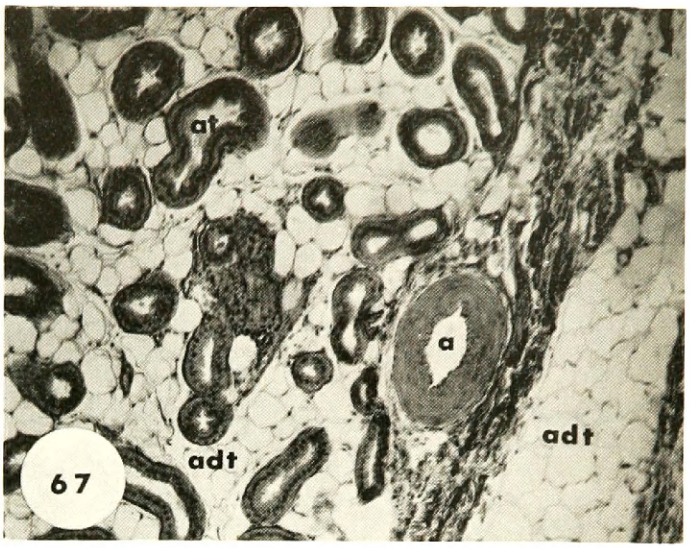
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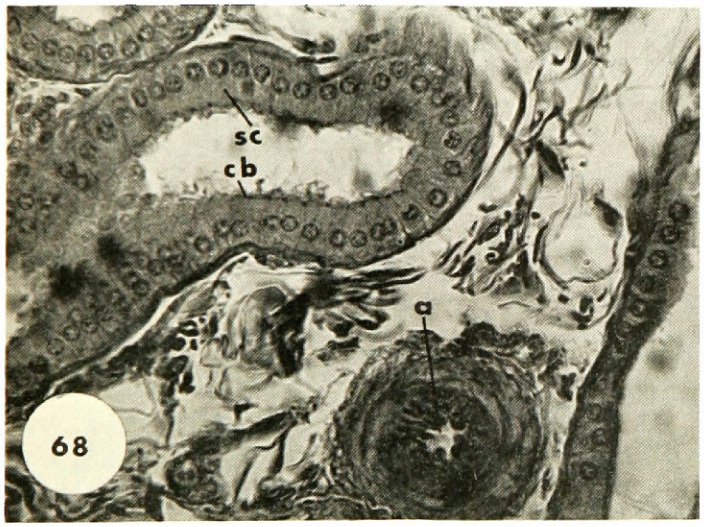
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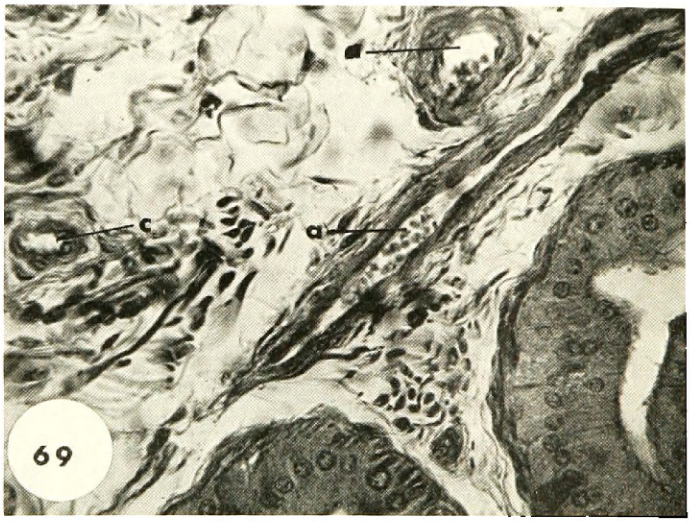
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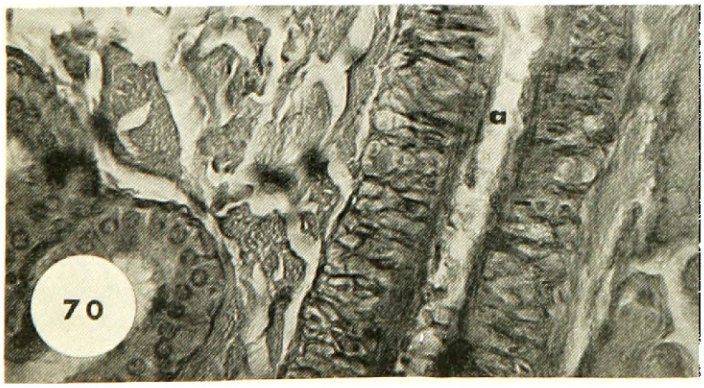
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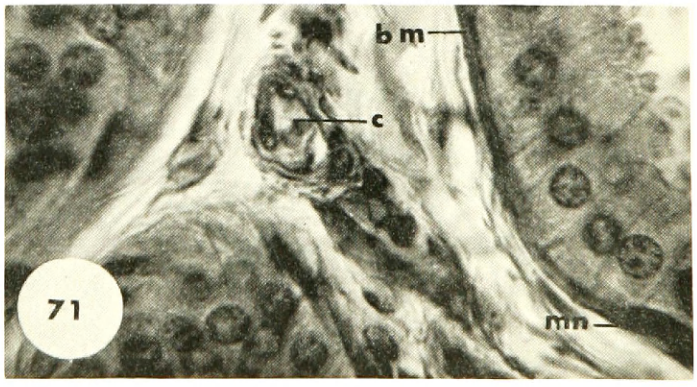
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Explanation of Figures

Figure 72. The only regressed apocrine tubules (rt) of the rump glands examined were observed in female rump gland 68-10. Approx. 34 X.

Figure 73. Rump gland 68-10. Tubules (t) adjacent to the regressed tubules (rt) are well-developed. Approx. 84 X.

Figure 74. Rump gland 68-10. The lumen of the regressed tubules are partially or completely closed and the secretory cells stain darker and their nuclei are distorted. Approx. 383 X.

Figure 75. Rump gland H3082. Notice the denser connective tissue and the fewer adipose tissue of the lower zone (lz). Hair follicles penetrate deep into the apocrine zone. Hair papilla (hp). Artery (a). Approx. 84 X.

Figure 76. Rump gland H3082. This apocrine excretory duct (ed) is lined by one and two layers of cuboidal epithelium. Approx. 383 X.

Figure 77. Rump gland 61-1. The apocrine excretory duct (ed) becomes funnel-shaped as it nears the hair follicle. Approx. 383 X.


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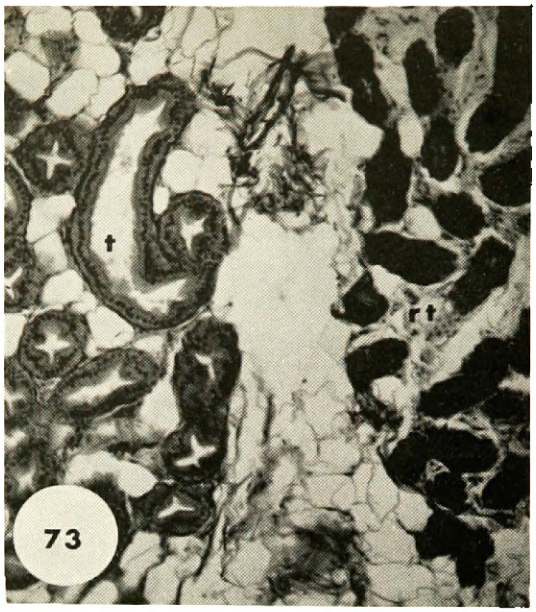
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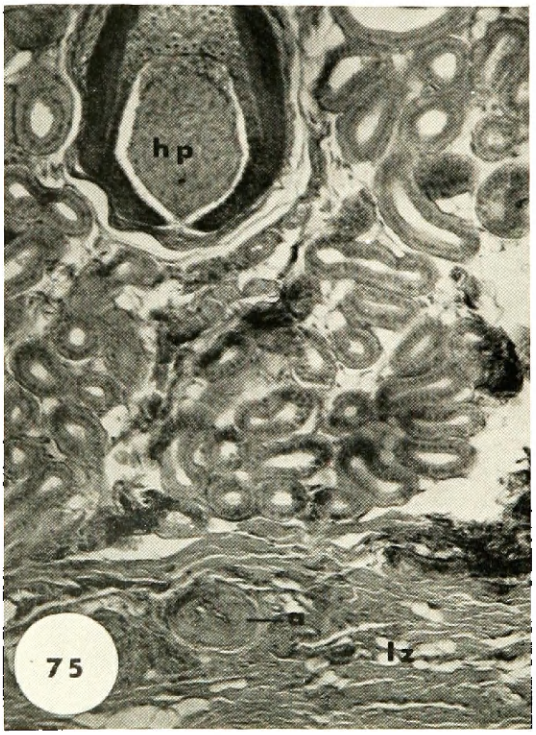
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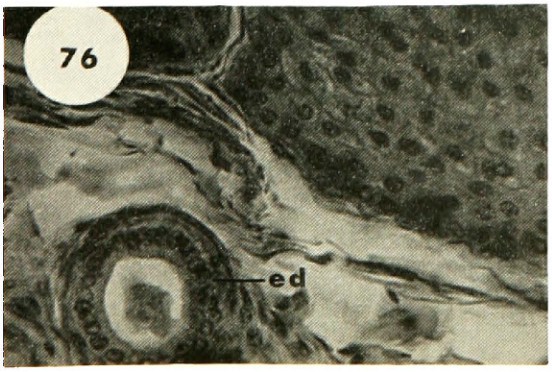
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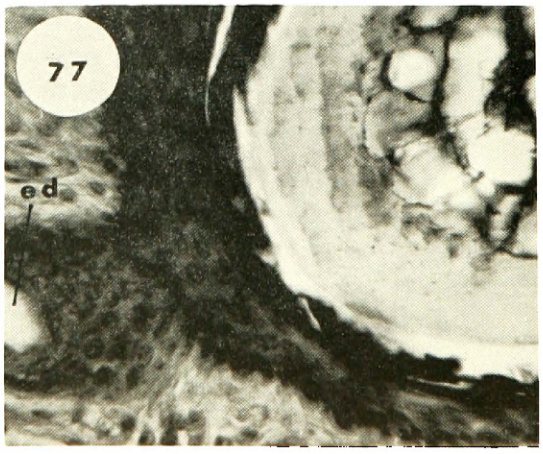
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Histology of the Female Subauricular Skin

The skin patch below the ear of the female pronghorn has no glandular area similar to the subauricular gland of the males. This patch is histologically similar to typical antelope skin described in the next section.

The hairs of this area are long and light in color. The center of the patch has gray to tan colored hairs with surrounding lighter gray and white ones. The skin is composed of a thin pigmented epidermis 10-30 μ thick. Short, thick hair follicles penetrate the dermis to a maximum depth of approximately 1.35 mm. Among the hair follicles are a few scattered and slightly differentiated sebaceous units (Figures 78 and 80). They are associated with the hair follicles and secrete into the pilosebaceous canal. Intermixed with the sebaceous glands are a few short eccrine type sweat glands. Their excretory ducts are lined by a double layer of cuboidal cells and empty directly onto the skin surface. All the sebaceous and eccrine glands are found within 0.50 mm. of the skin's surface.

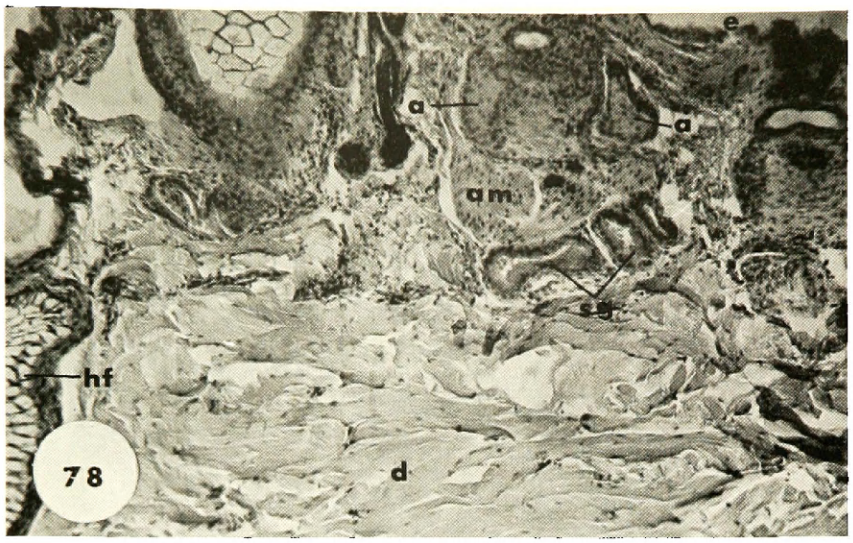
The glands are surrounded by irregularly arranged dense connective tissue. The arrector pili muscles are short and stubby. The underlying dermis consists of dense wavy bundles of collagenous fibers. Large arterioles run along the basal protion of this layer.

Explanation of Figures

Figure 78. The subauricular skin from the doe pronghorn 68-10 reveals scattered eccrine sweat glands (sg) and small, slightly differentiated sebaceous acini (a). Notice the large arrector pili muscles (am) and the thick collagenous tissue of the dermis (d). Hair follicle (hf). Epidermis (e). Approx. 84 X.

Figure 79. The abdominal skin from pronghorn 69-1 shows short diagonal hair follicles (hf), few eccrine sweat glands (sg) and a thick dermis (d). Approx. 84 X.

Figure 80. An eccrine sweat gland (sg) and slightly differentiated acinus (a) from the subauricular skin of the doe pronghorn 68-10. Accumulation of minute lipid vacuoles in the central cells (cc). Approx. 383 X.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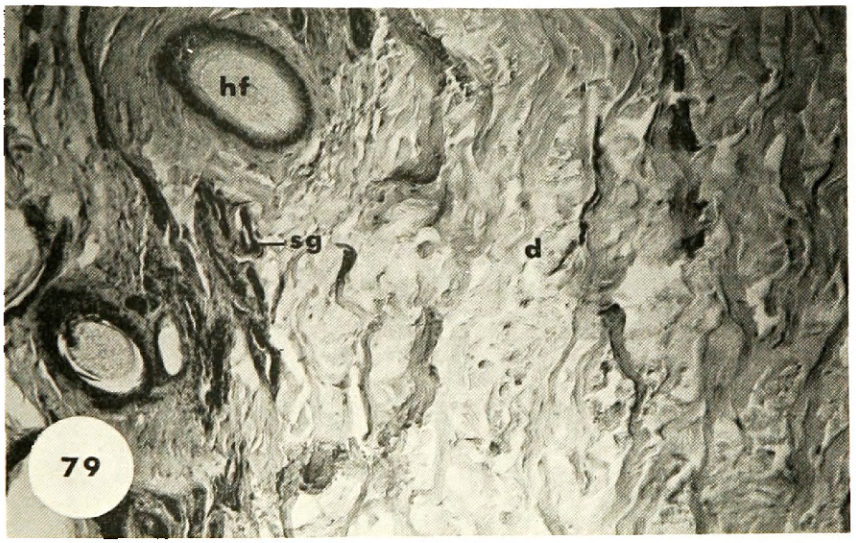
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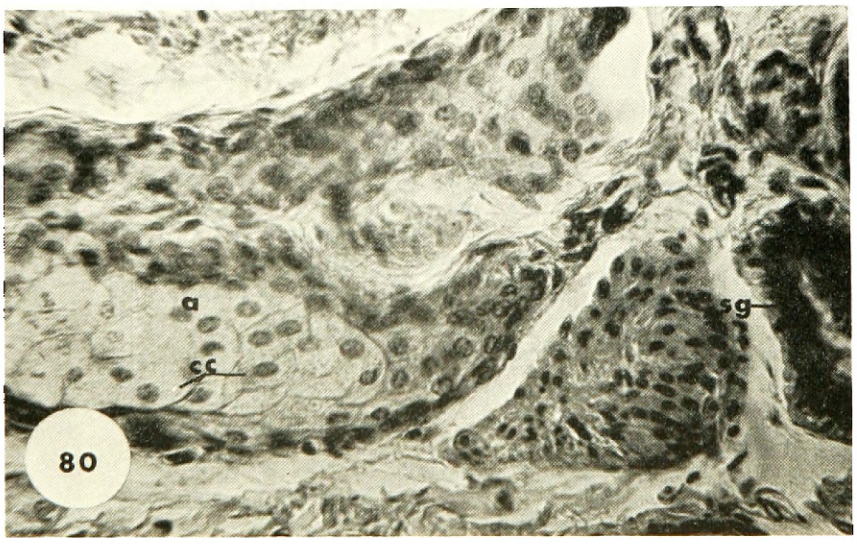
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Histology of Pronghorn Skin

Pronghorn skin from the abdomen and areas adjacent to the subauricular and rump glands were examined and found to be histologically similar to each other and to the subauricular skin patch of the female.

The epidermis has small surface ridges and is composed of a thin stratum germinativum (1-2 cells thick) and thicker layers of dry cornified tissue of the stratum disjunctum and stratum corneum. The skin reveals a few scattered eccrine sweat glands and slightly differentiated sebaceous units (Figure 79).

Very dense collagenous and elastic tissue imbeds the short, thick and diagonal hair follicles. Minute hair follicles, measuring 13 μ in diameter, are usually associated with the larger follicles.

Comparison of the Subauricular Gland of Normal and Castrated Pronghorn

By comparing the glandular measurements and secretory activity of the normal (61-4) and castrated (H3561 and H3082) glands of pronghorns of the same month, it is apparent that the glands of the castrates are reduced (Table X). The castrates, especially gland H3082, are similar in most respects to the regressed and inactive gland of the December animal (61-8) (Table X). Androgens apparently play an important role in the proliferation and maintenance of the subauricular gland.

TABLE X

Comparison of the Subauricular Glands from Two Castrated Pronghorns from August and Two Normal Pronghorns, one from August and one from December

	N 61-4 (Aug)		C H3561 (Aug)		C H3082 (Aug)		N 61-8 (Dec)	
Reticular Zone Height in mm.	1.30		.50		.40		.65	
Apocrine Zone Height in mm.	3.94		.35		.45		.78	
Sebaceous Zone Height in mm.	3.25		.50		.60		.84	
Hair Follicle Depth in mm.	4.00		2.00		1.90		1.40	
	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.	$\bar{X}$	S.D.
Apocrine Cell Height in μ	17.12	±3.31	15.62	±1.86	12.03	±1.97	12.32	±4.42
Apocrine Tubule diameter in μ	80.19	±12.87	51.04	±9.24	49.19	±9.61	45.25	±8.02
Apocrine Lumen diameter in μ	43.94	±12.01	24.24	±4.92	21.73	±7.94	22.08	±7.89
Estimation of Apocrine Activity*	++++		+		+		+	
Estimation of Sebaceous Activity*	++++		+		+		+	

$\bar{X}$ = Mean
+ = Poor Activity
S.D. = Standard deviation
++ = Moderate Activity
++++ = Extremely Active Activity
0 = no Activity
+++ = Active Activity

*Criteria used for the Estimation of the glandular activity are mentioned in Table V.

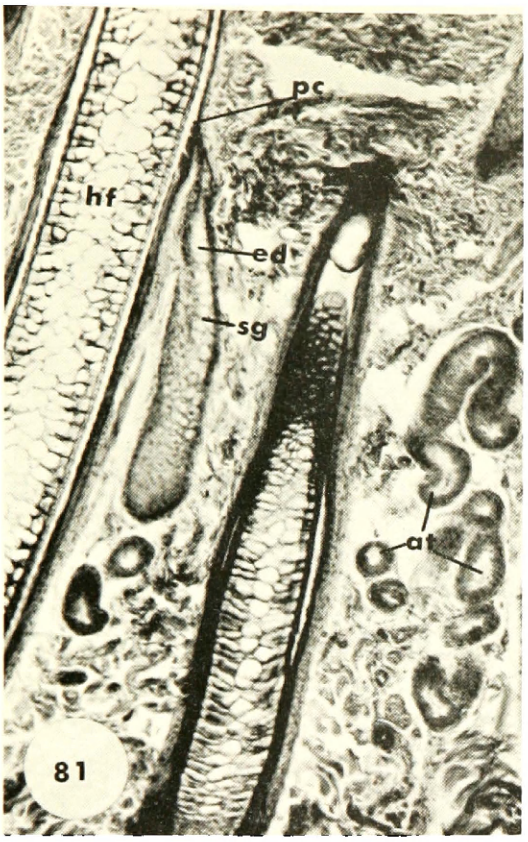
Explanation of Figures

Figure 81. Subauricular gland H3561 from a castrated pronghorn shows a few scattered apocrine (at) and sebaceous glands (sg). Compare with normal pronghorn's subauricular gland 61-4 from the same month, represented in Figures 16, 20, 35, 36, and 37. Notice the sebaceous excretory duct (ed), emptying into the pilosebaceous canal (pc). Dense connective tissue surrounds the glandular components. Hair follicle (hf). Approx. 84 X.

Figure 82. Subauricular gland H3082 from a castrated pronghorn shows more apocrine (at) and sebaceous glands (sg) than the castrated animal H3561, represented in Figure 81. Hair papilla (hp). Approx. 84 X.

Figure 83. Subauricular gland H3561 from a castrated animal. The inactive and regressed apocrine tubules. Notice the dense connective tissue around the tubules and the arrector pili muscle (am). Approx. 383 X.

Figure 84. Slightly more differentiated acini (a) and better developed apocrine tubules (at) in subauricular gland H3082 than was demonstrated in subauricular gland H3561, represented in Figures 81 and 83. Subauricular gland H3082 from a castrated pronghorn. Approx. 383 X.



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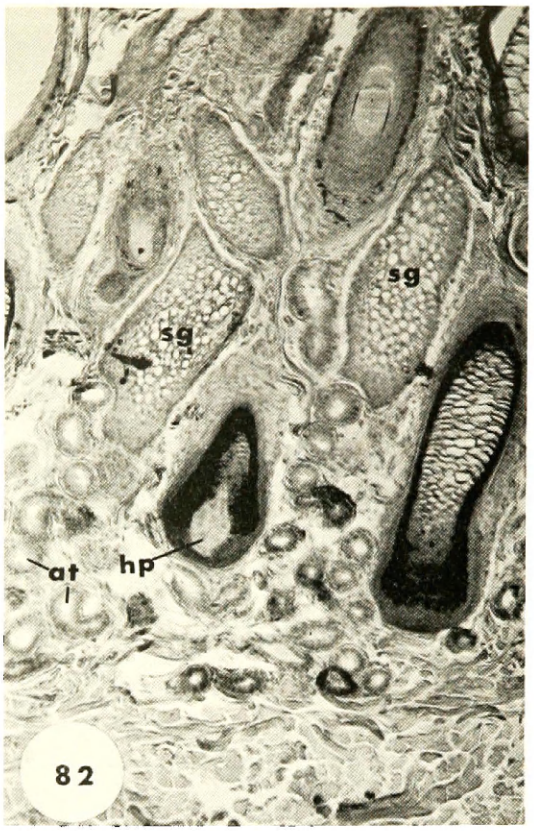

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Animal H3561 was castrated as a fawn and four years lapsed before it was collected. This might explain the reason why there are fewer sudoriferous and sebaceous units in its glands compared to animal H3082 which was castrated as an adult, two years before it was collected. The few glandular units are located between the hair follicles of gland H3561 but are comparatively numerous in gland H3082, which also has apocrine tubules surrounding the basal portion of the hair follicle.

Comparison of the Rump and Subauricular Glands and Further Comments on the Glands of the Castrated Pronghorns

The rump and subauricular glands are basically composed of sebaceous and apocrine components. Yet, the two skin glands appear to serve different functions and are controlled by different mechanisms. Even the basic glandular components are histologically different.

The apocrine and sebaceous components of the rump gland secrete constantly at a slow rate throughout the year without any significant alterations in histology or size. The subauricular gland drastically changes in its activity, glandular dimensions, and histology (Tables III, V and VI).

For detailed comparison of the two glands, the following measurements are compared: the height of the sebaceous zone, the height of the apocrine zone, the diameter of the apocrine tubule and lumen, and the height of the

apocrine secretory epithelium.

The height of the sebaceous zone of the rump gland is maintained at the same approximate level throughout the year while the zone of the subauricular gland undergoes profound proliferation and regression (Figures 85 and 86). The peak of proliferation for the subauricular gland appears in the summer months and reaches a minimum in December and January. The sebaceous zone of the rump gland from the castrated animals is within the established range of the sebaceous zone of normal pronghorn (Figure 86). The sebaceous zone of the subauricular gland from the August castrated animals is not comparable to the zone height of the normal animal from the same month, but is comparable to the zone of the December and January animals.

The approximate height of the apocrine zone for both glands from each month has a trend similar to that described for their sebaceous zone (Figures 87 and 88) although the apocrine zone of the subauricular gland does undergo a more profound change (Figures 87 and 88). Subauricular glands from castrated animals have smaller apocrine zones than were noted for the inactive January and December glands. The peak of apocrine development in the subauricular gland appears in June, approximating the peak of sebaceous development.

The mean, standard deviation, and 95% confidence level of the standard error for the approximate diameter of

the apocrine tubules and lumens, and the approximate height of secretory cells for both glands for each month has a trend similar to what was described for the apocrine zones (Figures 89 to 94). The apocrine measurements for the subauricular glands from castrated pronghorns (collected in August) show smaller dimensions than are characteristic for that month. The relative constancy of the height of the apocrine tubules, lumens, and secretory cells in the rump glands of the male, female, and the castrated antelope, suggests that this gland secretes at a constant rate throughout the year and is not affected by sex hormones.

The large apocrine tubules, lumens, and secretory cells of the rump glands are only achieved during the proliferating and active secretory stages of the subauricular glands of males. The apocrine portion of the rump gland constantly maintains these large dimensions and has a very low secretory discharge; but when the apocrine portion of the subauricular glands attains the large dimensions, its discharge is great. Bloom and Fawcett (1968) report that the shape of the free lumen of the secretory portion of apocrine tubules in general fluctuates greatly with the functional state of the gland. This is apparent in the subauricular gland but not in the rump gland.

The subauricular gland of animal 68-2, collected in February, shows greater development than one would expect. The warmer than normal spring conditions under which this animal was collected may have initiated earlier development.

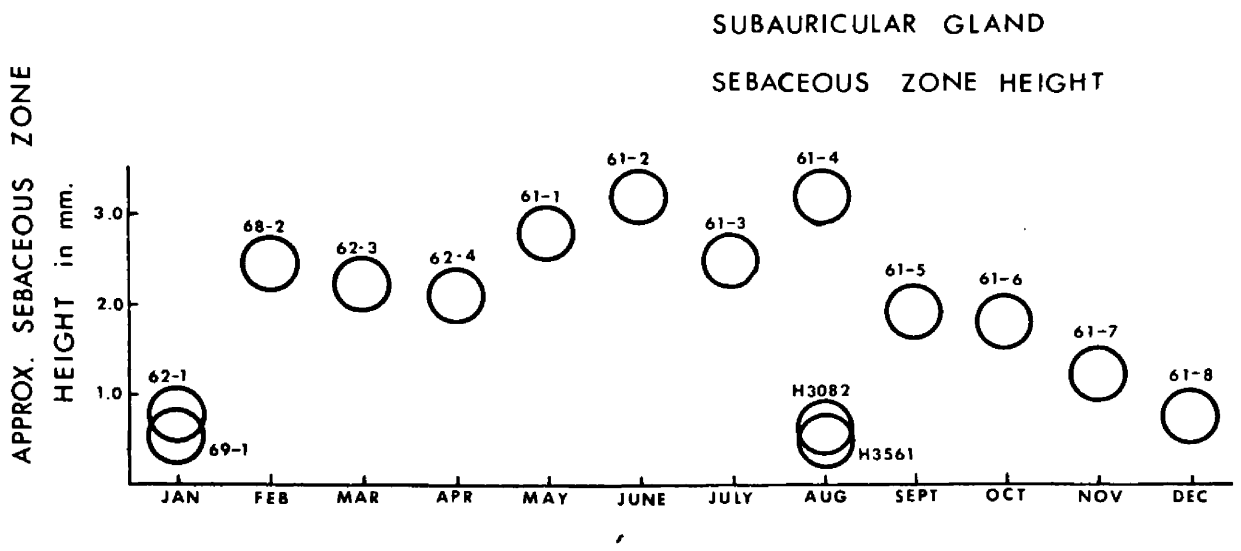


Figure 85

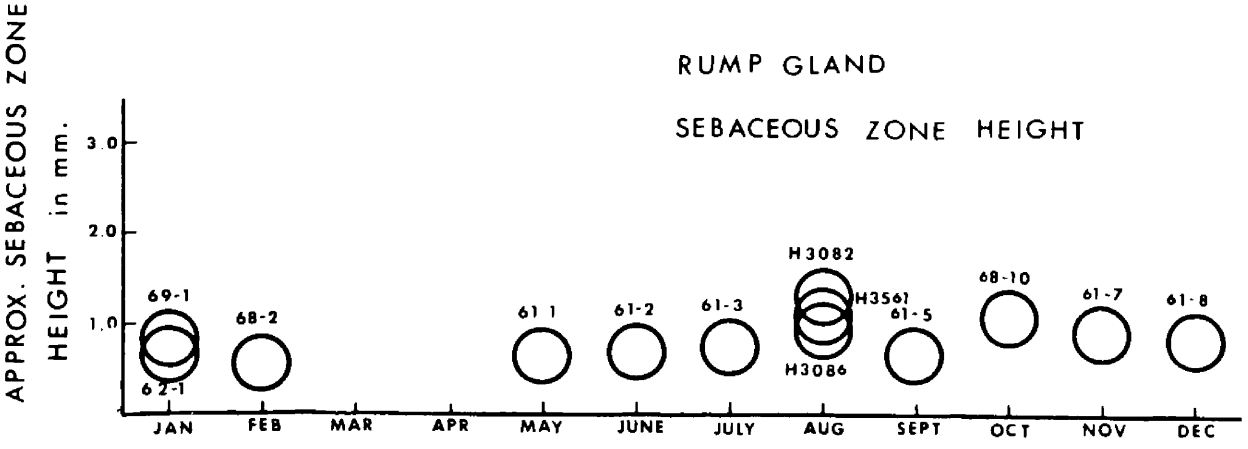
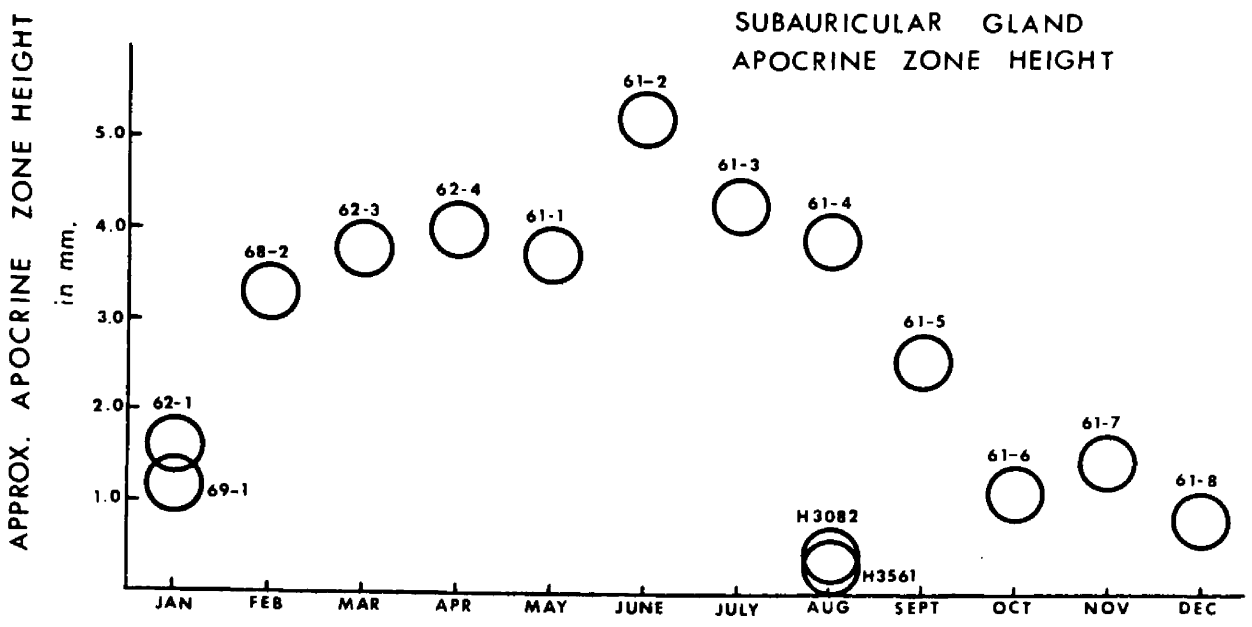


Figure 86



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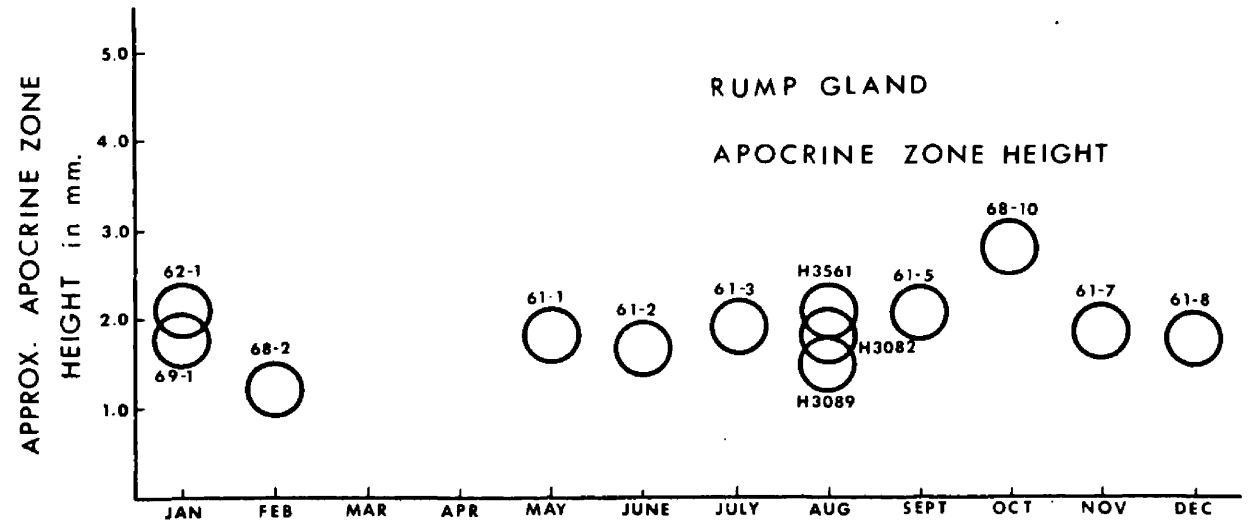

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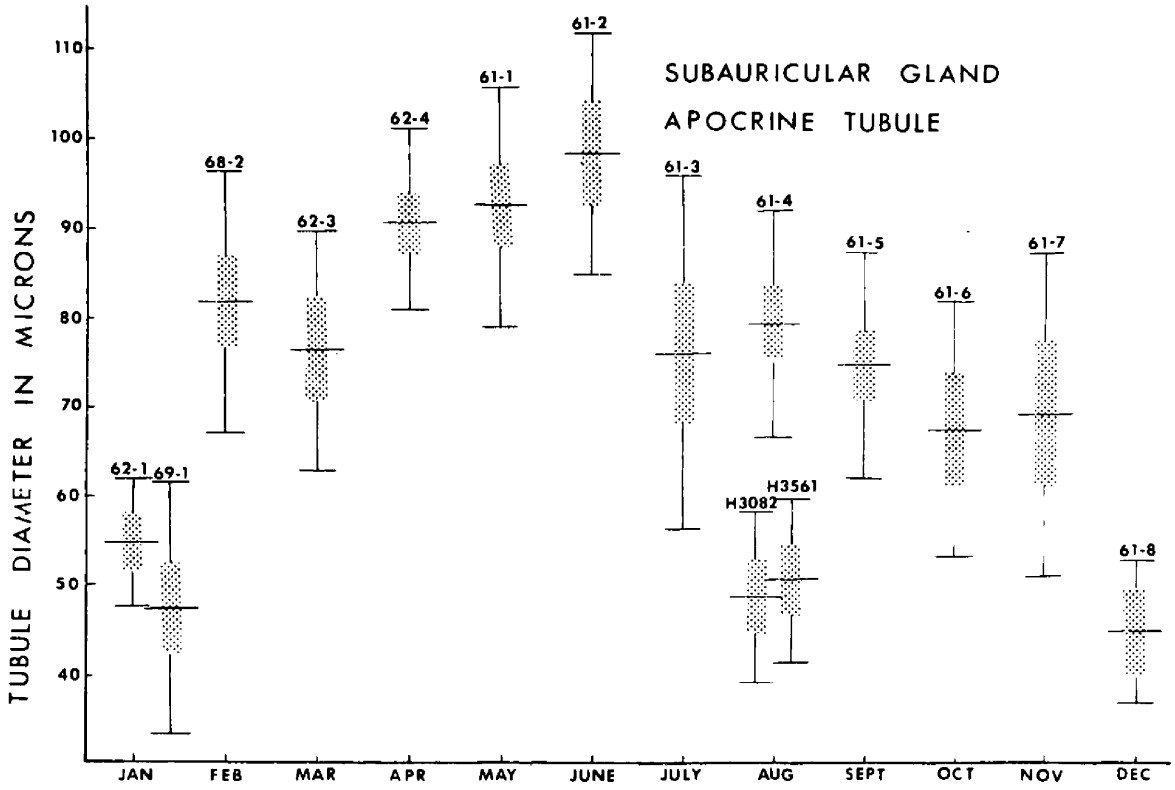

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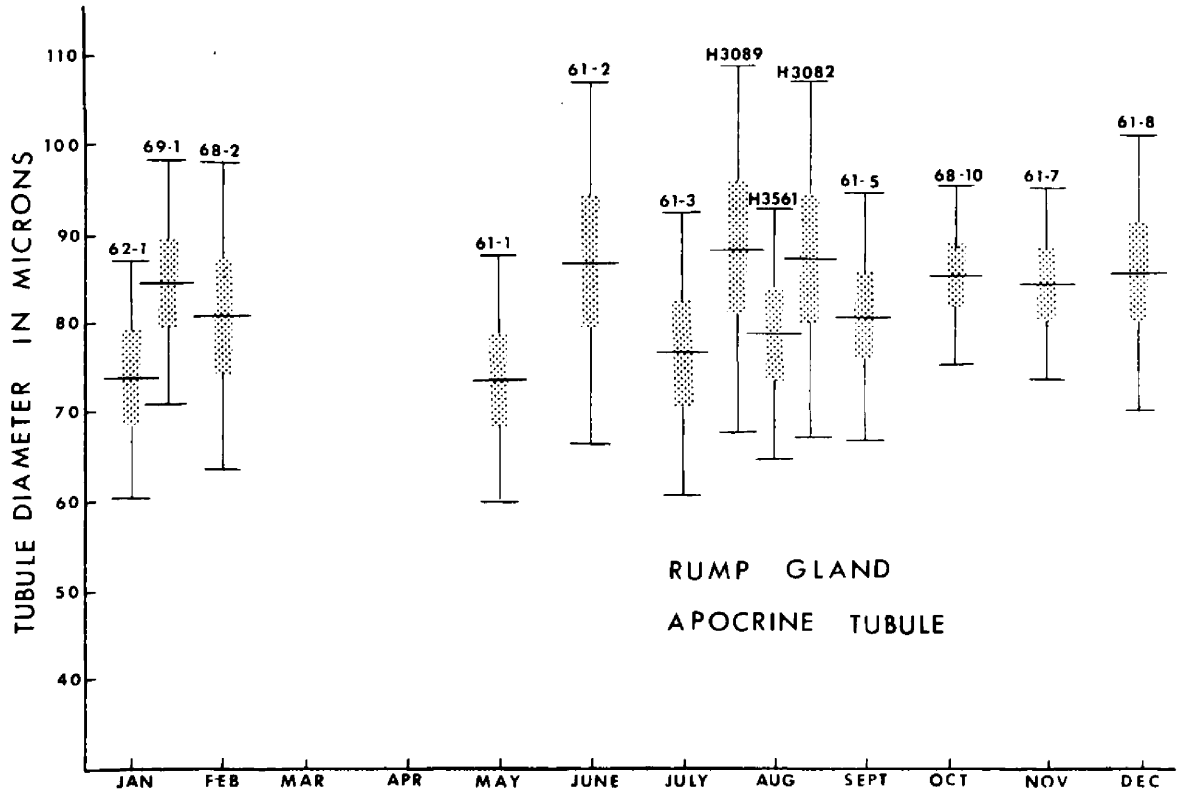

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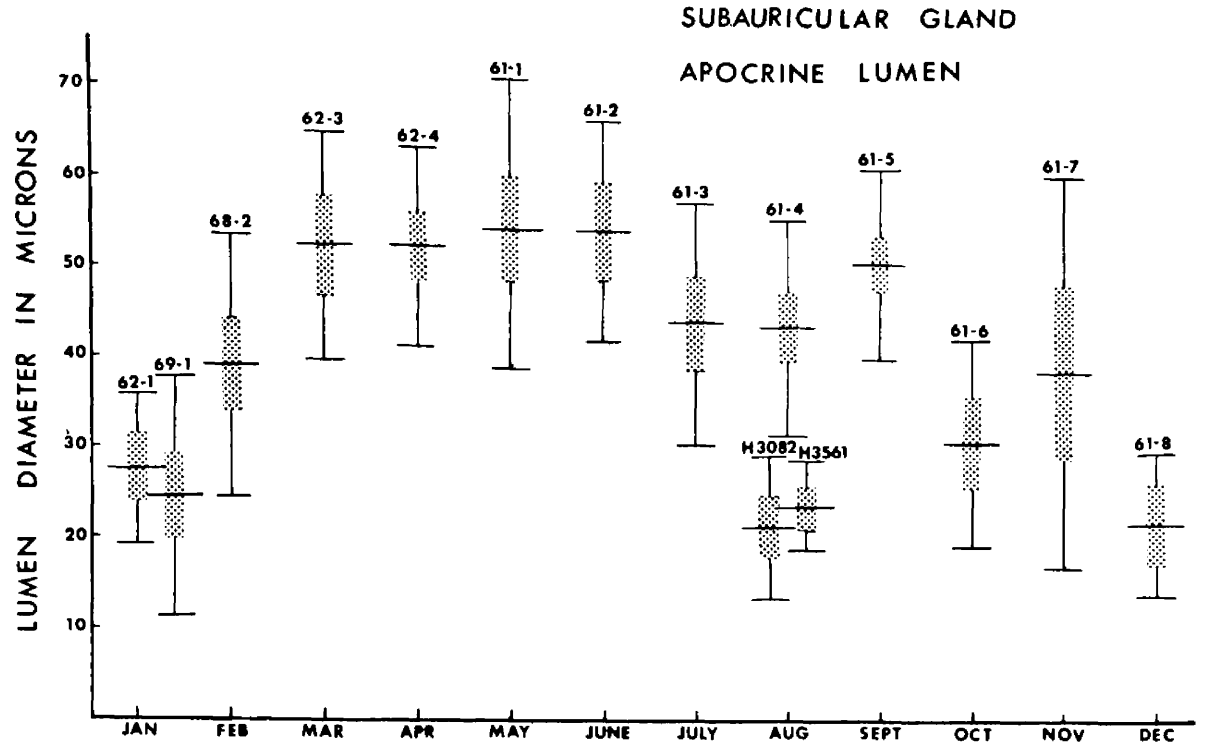

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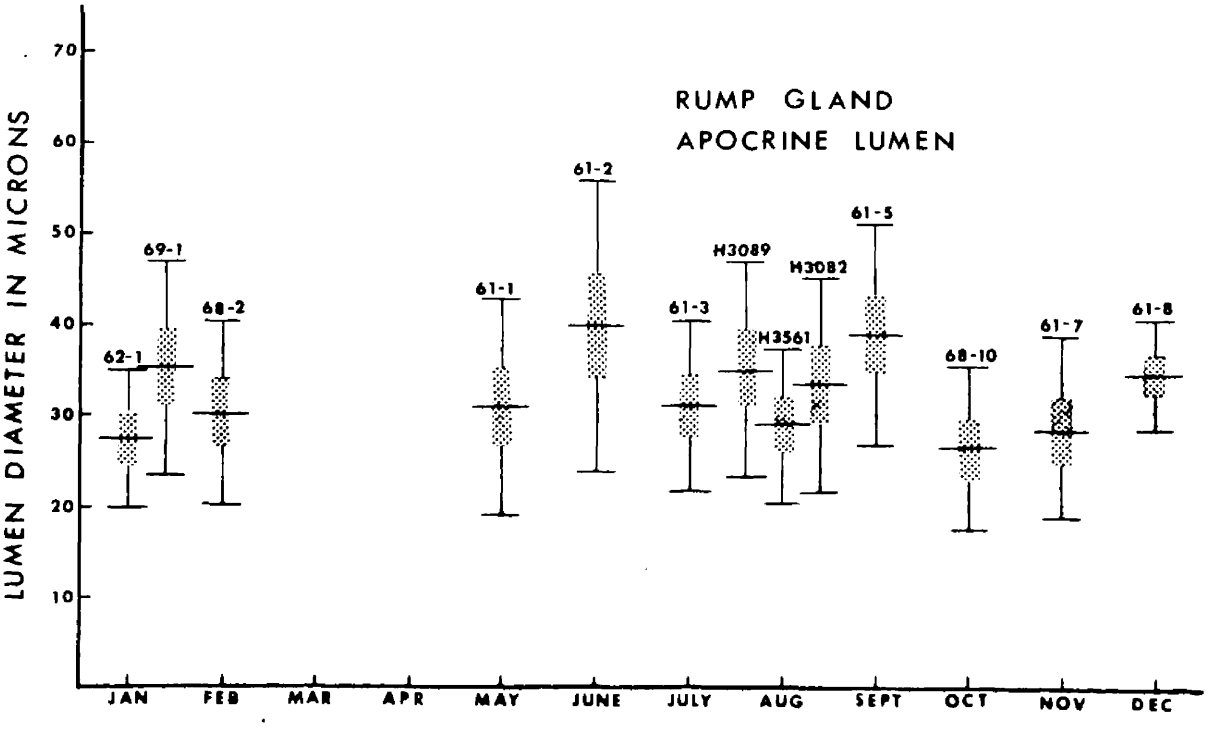

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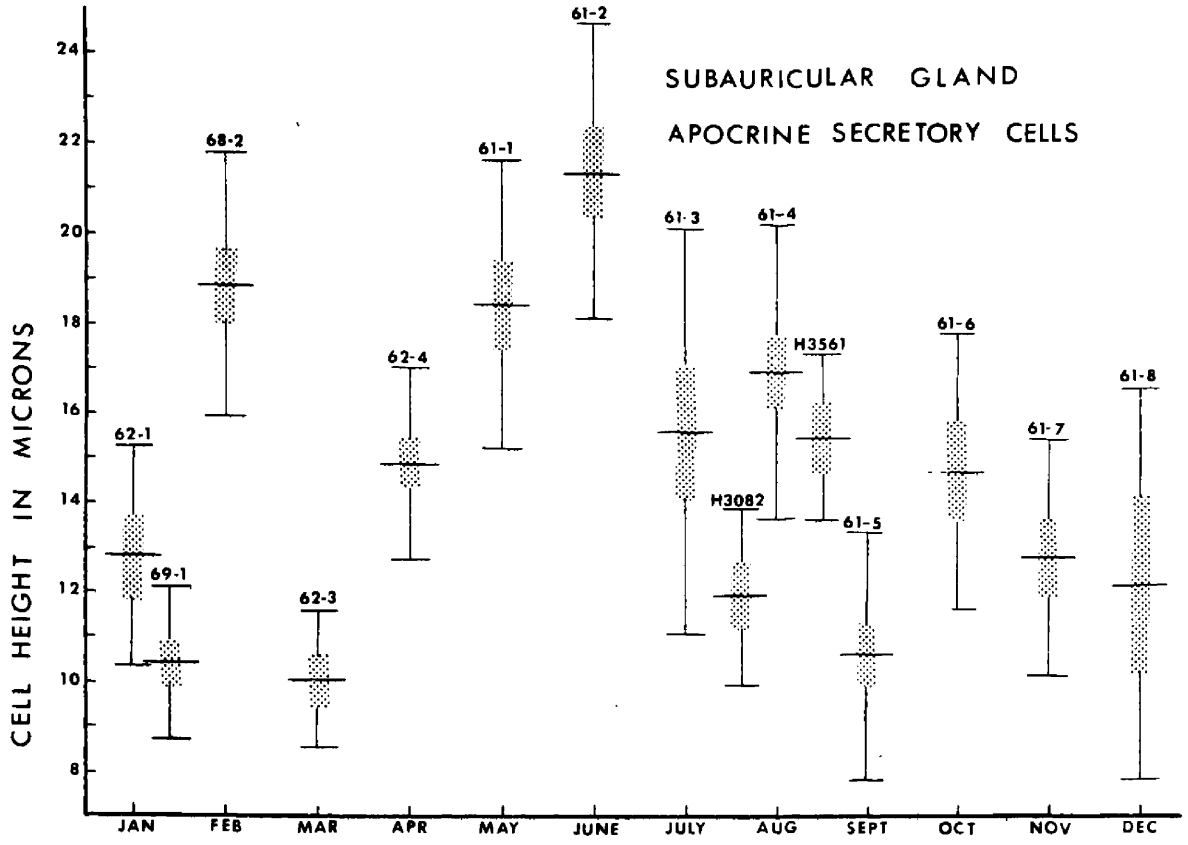

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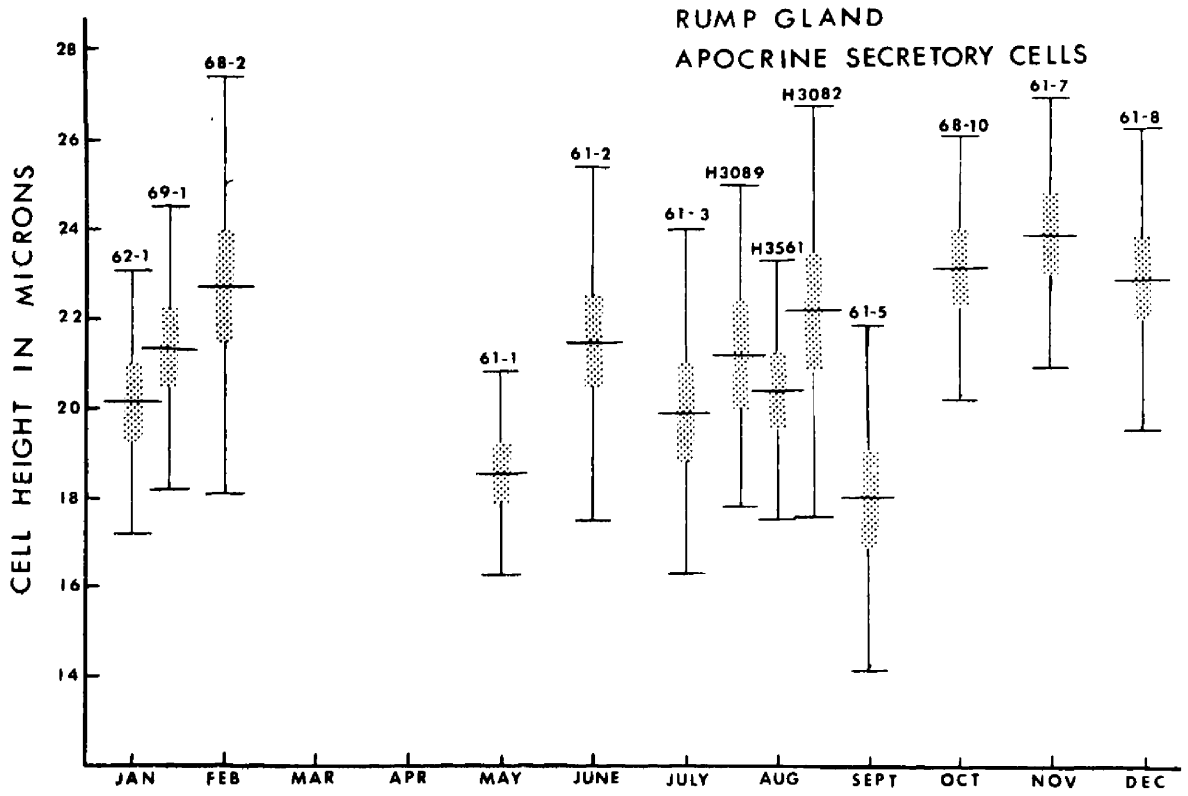


Figure 94

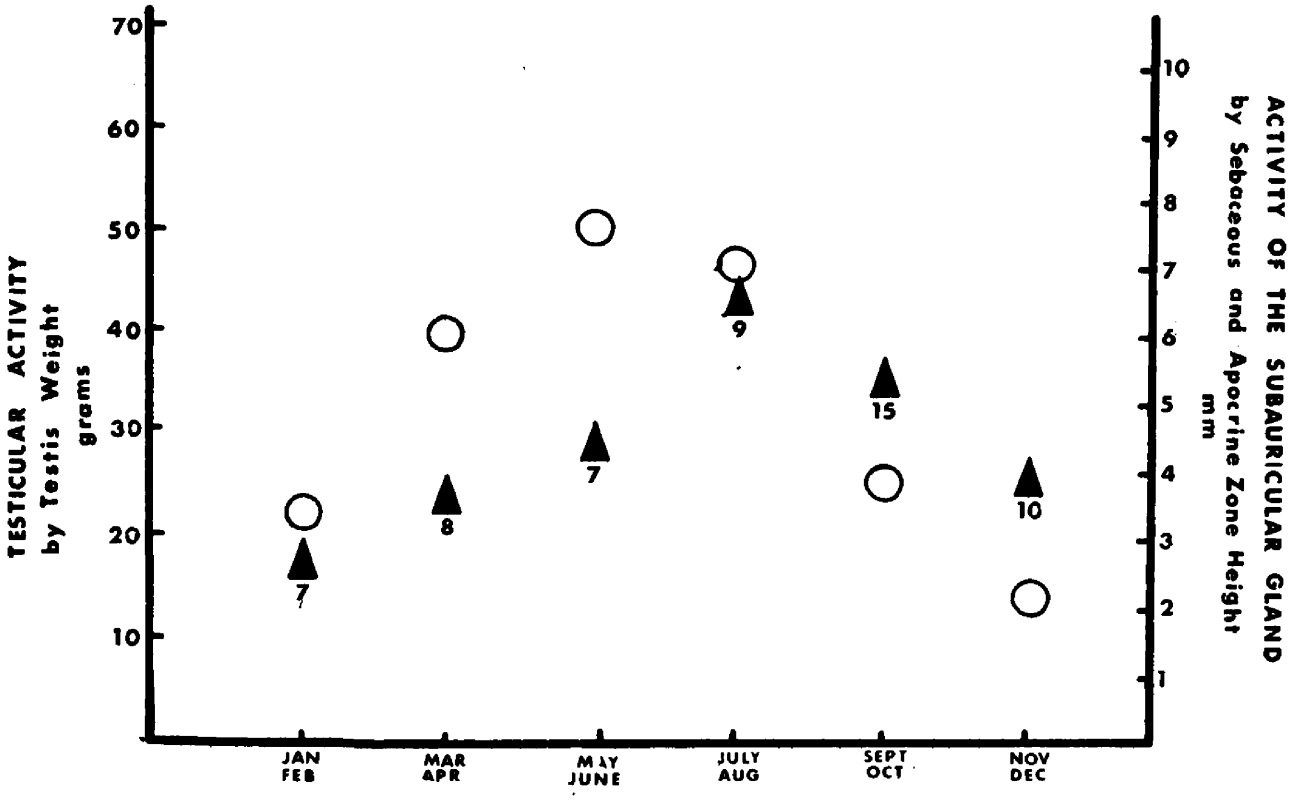
Relationships between Subauricular Gland and Testicular Activity

Several observers have suspected that the activity of the subauricular gland is related to the breeding season. I have established that glands are reduced and inactive in castrated bucks from August, but that the glands from normal bucks from the same month are large and active. This would suggest that this gland is hormonally controlled by the testes.

O'Gara and Moy (unpublished) determined monthly variation in testicular activity and size. This study indicates that testes begin to gain weight in March and April and reach a maximum weight in July and August. Spermatogenesis and enlargement of the interstitial cells begin in February and March, and reach a peak in July and August. Sperm are found in the lumens of the seminiferous tubules as late as December. Pronghorns ordinarily breed during a limited time in September and October (Skinner, 1922) which is after the climax of testicular activity.

By combining the graphs of testis weight against time, to indicate testicular activity, with the graph of combined height of the sebaceous and apocrine zones of the subauricular gland against time, to indicate its secretory activity, a correlation is indicated (Figure 114). (O'Gara and I have determined the mean testis size for each month.) The peak of activity of the gland appears to be

Figure 114



ACTIVITY OF THE SUBAURICULAR GLAND = ○

TESTICULAR ACTIVITY = ▲ 7 MEAN SAMPLE SIZE

closely related to the peak of testicular activity. The presence of large sebaceous vessicles and the large amounts of secretory material in the apocrine lumens of the August glands support this hypothesis. Breeding takes place shortly after the climax of the testicular activity and the activity of the subauricular gland. The presence of slight testicular activity in February and March can explain the early proliferation of the gland. Androgens have been demonstrated to stimulate sebaceous activity and to cause a sharp increase in mitotic activity (Ebling, 1948; Montagna and Kenyin, 1949).

Unlike the subauricular gland the rump gland seems to follow Montagna's (1966) contention that hormones play an initial role in the development and maintenance of skin glands; but, once developed, they are relatively self-sufficient.

The Effect of Aging on the Glands

Quay (1955) and Montagna (1962) note that age usually has little or no effect upon the condition of the skin glands. No age differences were observed in comparing the subauricular and rump glands of two January animals--a yearling (62-1) and an eight-year old buck (69-1)--or in any of the other glands examined.

Possible Functions of the Rump and Subauricular Glands

Combining information from earlier workers about the rump, subauricular glands and other glands with information from the present study, I can speculate on some of the functions of the glands.

The location of the rump gland seemed ideal for quick air-born warning scent and may be an additional warning to the flashy visual communication of the erected rump patch. The location also suggests that the scent may be rubbed on taller vegetation for other animals to follow.

Sweat glands of Suncus murinus cause the musk production, not the sebaceous glands (Dryden and Conaway, 1967). Therefore, one might suspect that the apocrine sudoriferous glands produce the scent and combine with the sebum of the sebaceous gland to allow the scent to remain for some time. Such a gland would have to be maintained in a static state, which has already been established for the rump gland, and be capable of discharging scent instantaneously. The large size of the arrector pili muscles could facilitate instant secretion as well as hair erection. Also, the myoepithelial cells are best developed in the tubules that are lined by the tallest epithelium which is similar to the tubules of the rump gland (Montagna, 1962). These myoepithelial cells aid secretion.

Instant triggering of the scent from the glands could be induced by some component of the blood as the

tubules of the rump gland are richly supplied with vessels, or the autonomic nervous system might be the necessary triggering system.

Caton (1877) and Seton (1929) report that the subauricular gland seems to be related to the mating behavior of the buck, and all indications from this study point toward a function in breeding. Bromley (1969) postulated that one means by which male pronghorns can mark their territories during breeding season is by rubbing the scent of the subauricular gland on the fall vegetation.

Gross and Histological Description of the Fore- and Hindfoot Interdigital Glands

Caton (1877) gave the first description of the two fore- and two hindfoot interdigital glands of the pronghorn and he described the odor secreted as unpleasant and seeming to grow stronger with age. The only interdigital glands examined by me were dissected from the oldest antelope (69-1). The fore- and hindfoot interdigital glands are grossly and histologically similar and only slightly resemble the interdigital glands of other artiodactyls (Quay, 1955-57).

The interdigital glands lie between the primary digits of each hoof. They are not hairy skin glands located on the surface of the skin which are typical of the interdigital glands of the caribou and whitetail deer (Quay, 1955-59). The large glands of the pronghorn are shaped like a sock

and open directly onto the surface through a single large orifice (Figures 95 and 96). The lumen of the gland is filled with considerable white secretory material, suggesting that this gland is extremely active. The gross glandular measurements for both glands are similar (Appendix B).

The glands appear to develop by invagination of the epidermis because the single lumen of the glands are lined with thick epidermis. One of the interdigital glands of the caribou (Quay, 1955) and both of the whitetail deer (Quay, 1959) are in the shape of a shallow pocket, which indicates that these glands may be less evolved.

Numerous infolds of the epidermis penetrate the dermis and become the large common excretory ducts into which numerous sebaceous units empty (Figures 99 and 100). The thick superficial outer layers of the epidermis consist of compound layers of cornified cells released from the keratinized epithelium lining the lumen. The upper portion of some of the common excretory ducts are completely filled with layers of cornified tissue. The orifice of one excretory duct is 0.45 mm. in diameter. They are larger on the average than the common excretory duct found in the rump gland (Figures 99 and 100).

The stratum lucidum is 2-3 μ thick. Beneath it are two to four layers of flattened cells of the stratum granulosum, 7-15 nucleated cells thick. The epidermis of

the interdigital gland is considerably thicker than the epidermis of the rump and subauricular glands.

Fine collagenous and elastic fibers surround the sebaceous and apocrine glands. Beneath the glandular zone, the dermis changes to a denser stroma of heavier collagenous fibers (Figures 101 to 103). The interdigital gland consists mainly of numerous large, lobulated actively secreting sebaceous glands and a few scattered apocrine glands. The apocrine units are usually scattered along the bottom portion of the sebaceous glands (Figure 102). Similar arrangement of glands were found in the interdigital glands of the whitetail deer (Quay, 1959). However, interdigital glands of the caribou are composed of a large apocrine zone (Quay, 1955).

Each sebaceous unit consists of numerous acini that empty into one large common duct (Figures 97 and 98). Along the periphery of the acini are one or two layers of basal cells. The remaining portion of the acini consists of central cells in various degrees of differentiation. There is an accumulation of the minute lipid vacuoles that are characteristic of the large vacuoles found in the subauricular gland.

The large tubules of the apocrine portion are lined with cuboidal and columnar secretory cells. Large spherical nuclei are basal in location. Only a few apocrine secretory cells have cytoplasmic budding along its cuticular

border; and the lumens are filled with little secretory material. The apocrine excretory duct is lined by a double layer of cuboidal cells and empties into the common sebaceous excretory duct.

Numerous blood vessels supply the glandular area. Large arteries are located in the dermis outside the glandular area, mainly concentrated in the dorsal and ventral portion of the interdigital glands. Associated with these arteries are occasional sensory corpuscles and several large nerves; each being composed of numerous mylinated fibers (Figures 95, 101 to 103). Quay (1955 and 1959) reported large arrector pili muscles associated with the hair follicles and sebaceous units of the caribou and whitetail deer interdigital glands which serve for hair erection and sebaceous secretion. No muscles or hair follicles are found in this gland of the pronghorn. The rump and subauricular glands have neither large arteries, corpuscles, or obvious nerves, nor are they reported for the interdigital glands of whitetail deer and caribou.

Sebum is produced by the sebaceous glands and appears to be the main product of the interdigital glands. The function of the gland, implied by its location between the digits of the hoof, could be to leave a scent in the vicinity. The sebum would allow the scent to remain for some time. Further study of monthly gland samples is necessary before any further functions can be postulated for the interdigital glands.

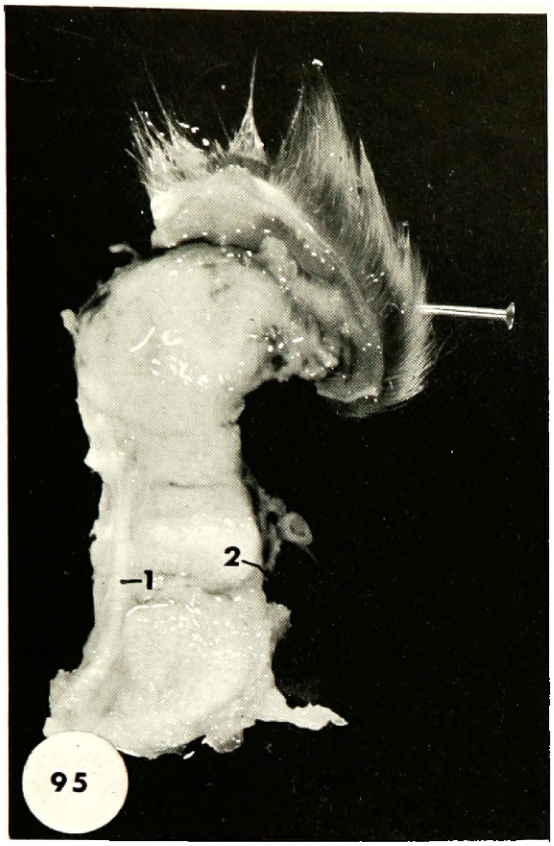
Explanation of Figures

Figure 95. Forefoot interdigital gland 69-1. The forefoot interdigital gland dissected from between the primary digits. Notice the sock-shape of the gland. The pin is in the gland's surface opening. Large arteries and nerves are found along the dorsal and ventral parts of the glands (1 and 2). Approx. 1 X.

Figure 96. The hindfoot interdigital gland 69-1. Notice the gross similarity between the interdigital glands. The pin is placed in the gland's opening. Approx. 1 X.

Figure 97. Hindfoot interdigital gland of 69-1. The sebaceous acini (a) and apocrine tubules (at) are stained with Sudan B and sectioned at 25 μ. Approx. 84 X.

Figure 98. Forefoot interdigital gland 69-1. The large sebaceous acini (a) emptying into the enormous excretory ducts (ed) lined by epidermal epithelium. Notice the large sebaceous cells. Dermis (d). Approx. 84 X.



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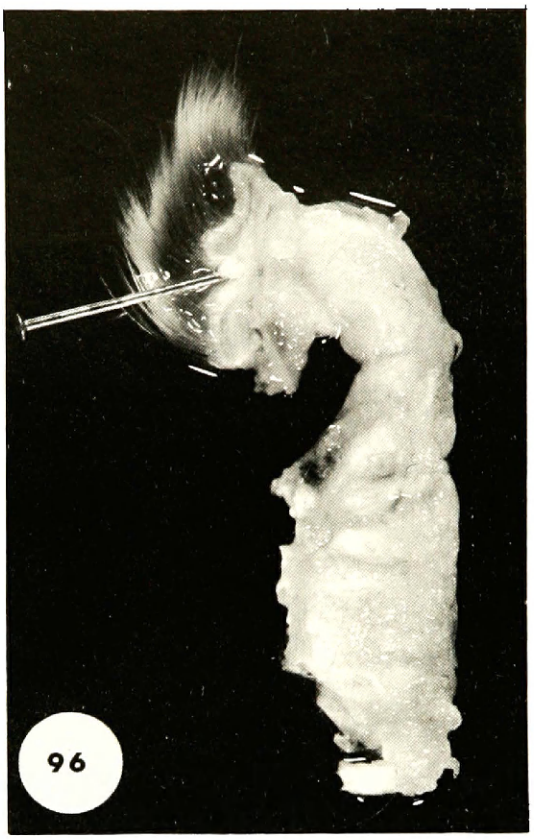

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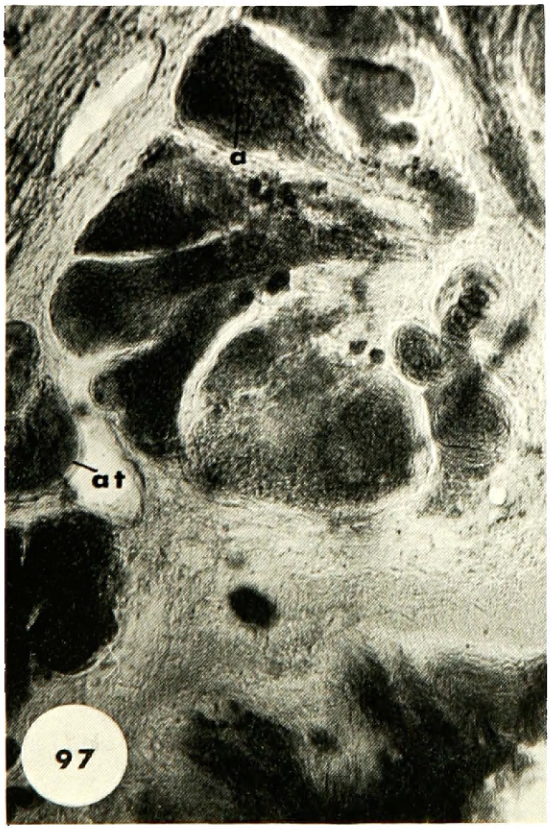

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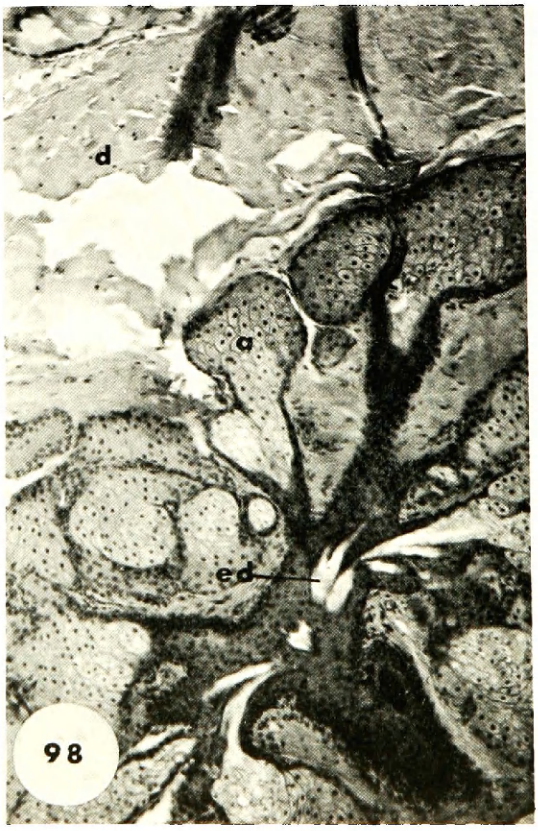

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Explanation of Figures

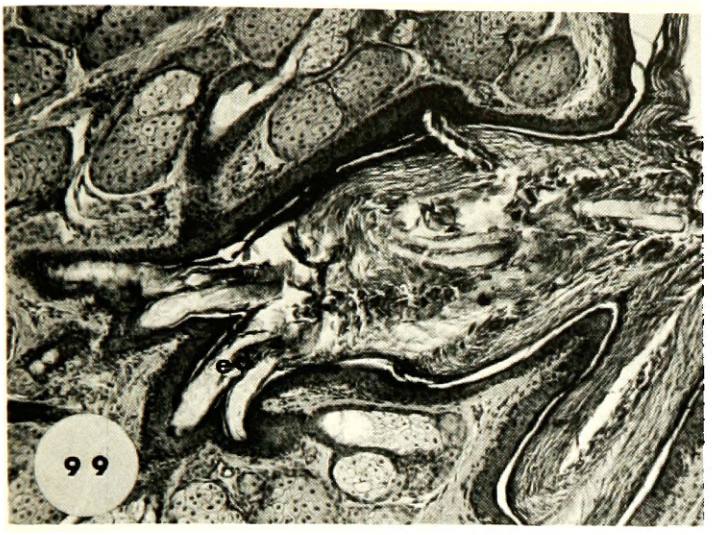
Figure 99. 100 Fore- and hindfoot interdigital gland 69-1. The thick epidermal infolds become the large common sebaceous excretory ducts (ed), and numerous acini empty into them. Notice the multi-layers of keratinized epithelium in the top portion of the ducts. Approx. 84 X.

Figure 101. Forefoot interdigital gland 69-1. Large artery (a) and arterioles (a) are found in the dermis that underlies the glandular zone. Approx. 84 X.

Figure 102. Hindfoot interdigital gland 69-1. Notice the few apocrine tubules (at) that are found along the bottom of the sebaceous units. Epidermis (e) and common excretory duct (ed). Approx. 84 X.

Figure 103. Hindfoot interdigital gland 69-1. Several nerves (n) are found associated with the arteries (a) in the dermis on the dorsal and ventral part of the interdigital glands. Approx. 84 X.

Figure 104. Forefoot interdigital gland 69-1. Nerves (n) and arterioles are located outside the sebaceous glandular zone. Approx. 84 X.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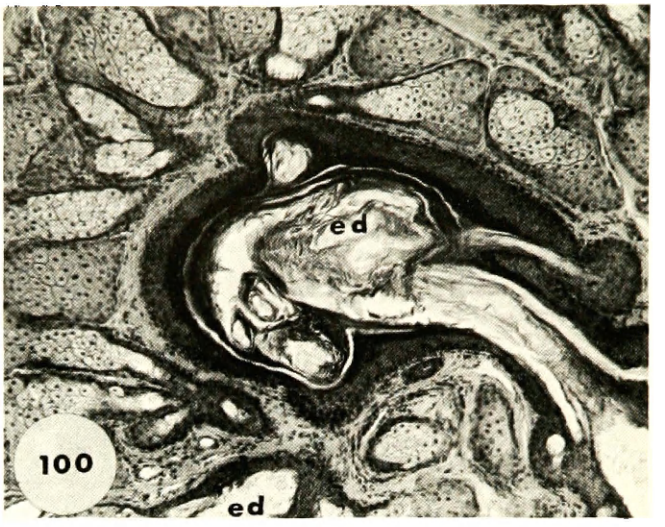
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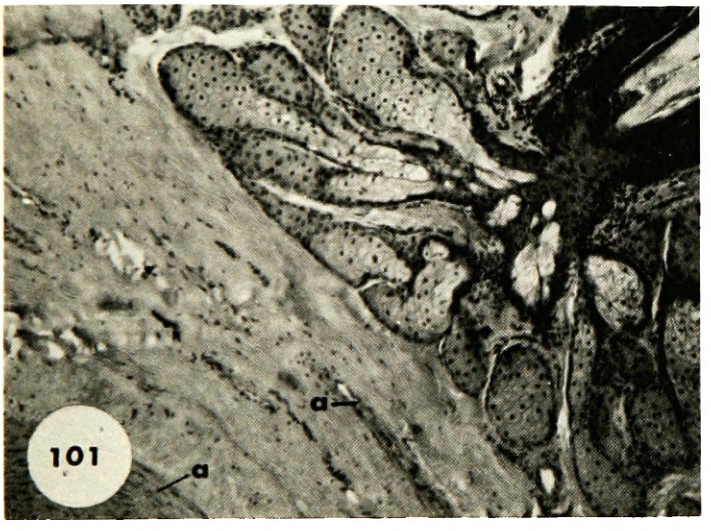
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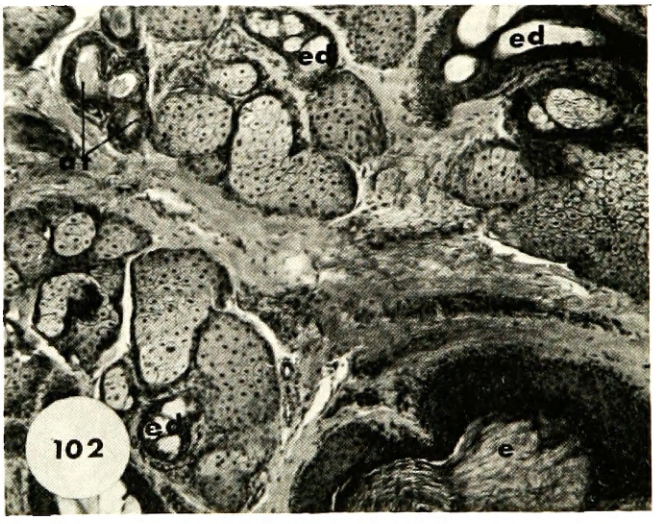
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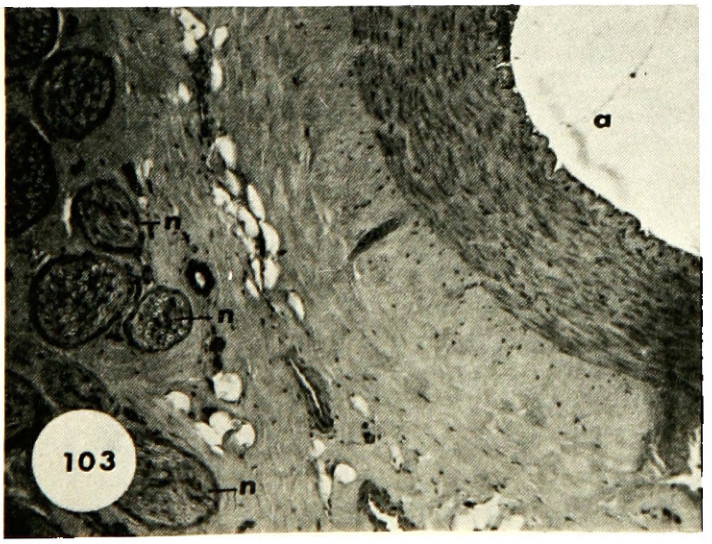
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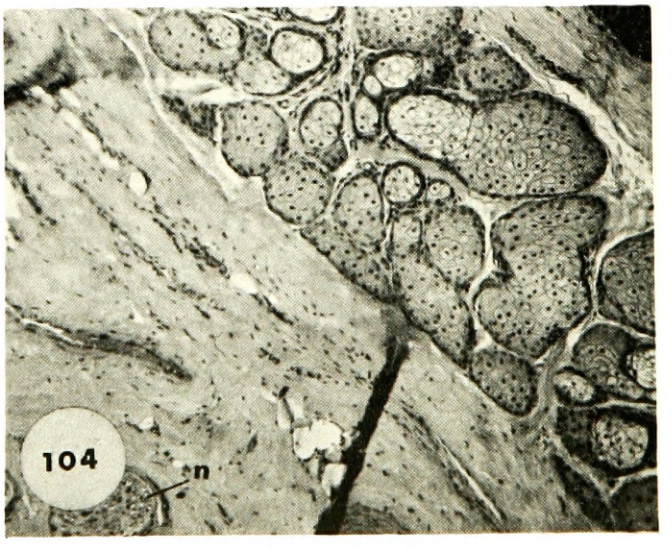
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Gross and Histological Description of the Median Gland

Caton (1877) briefly described the single median gland of the pronghorn and mentioned that it did not appear to be very active. The gland is located in the skin at the basal area of the spinal column where it meets the anterior edge of the white rump patch (Figure 105). The gland examined by me was from a pronghorn collected in January. Thin scattered hairs, whitish to tan in color, penetrate the skin of the gland at a slight angle, and are smaller than the thick, dark adjacent hairs (Figures 106 and 107).

The median gland, shaped like an ellipse, measures 60.0 mm. by 31.7 mm. at the greatest length and width. The maximum skin-gland thickness measures 6.50 mm. and the maximum glandular thickness is approximately 4.20 mm. The greatest glandular development is located at the center of the gland.

The median gland is composed of the same basic zones that are present in the subauricular and rump glands. Histologically, it resembles the rump gland more than the subauricular gland.

The epidermis is relatively thin, 15-30 μ in thickness. Numerous melanin granules are associated with the cells of the stratum germinativum layer. The root or papilla of the small hair follicles lies within the sebaceous zone and does not penetrate the apocrine zone as it does in the rump gland. Hair follicles, approximately 0.1 mm. in diameter,

penetrate to a depth of 1.3 mm. The large and numerous arrector pili muscles that are associated with the hairs have a maximum length of 1.0 mm. The muscles extend from the connective tissue sheath around the basal portion of the hair follicle to an area just beneath the epidermis (Figures 108-110).

The thin papillary layer of the dermis consists of abundant, fine collagenous fibers which give rise to the irregularly arranged bundles of thick collagenous tissue of the reticular zone (Figure 109).

The sebaceous zone ranges from 0.5 to 0.8 mm. thick and consists of scattered lobulated sebaceous units that are associated with each hair follicle, similar to the rump gland, except that they have fewer acini per sebaceous unit (Figures 109-110). The activity of the sebaceous gland resembles the activity of the subauricular gland in that the acini are quite mature, and the lipid material gradually accumulates to form large lipid vacuoles. The common excretory ducts of the sebaceous glands are small and are lined by epithelium that is continuous with the pilosebaceous canal into which they empty.

The apocrine zone is composed of tightly coiled tubules that have large dilated lumens (Figure 111). The zone ranges from 1.3-1.7 mm. in thickness. The secretory epithelium of the tubules ranges from low to high cuboidal cells (Figure 112). The luminal membrane reveals a few

Explanation of Figures

Figure 105. The median gland 69-1. The single median gland is located above the center of the rump patch. Notice the flattened arrangement of the hairs around the gland.

Figure 106. Median gland 69-1. A view of the surface of the median gland. Note the small secretory globules along the base of the hairs.

Figure 107. Cross-section through the center of median gland 69-1. Notice the sparse hairs and glandular zone (gz). Approx. 1 X.


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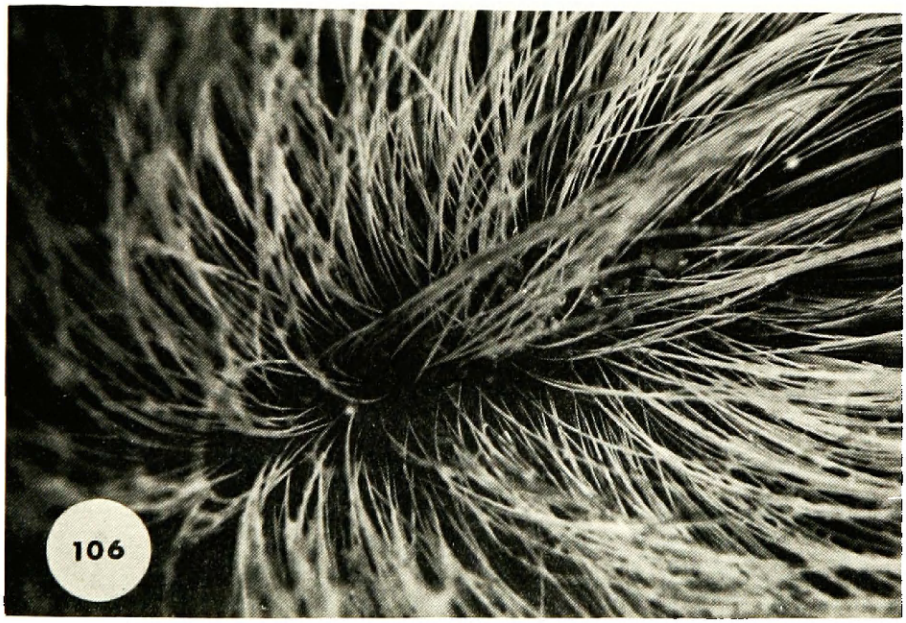
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Explanation of Figures

Figure 108. The outer layers portion of the median gland 69-1 are stained with Sudan B and sectioned at 25 μ. Epidermis (e) and sebaceous gland (sg) are colored black and are sudanophilic. Arrector pili muscle (am). Approx. 84 X.

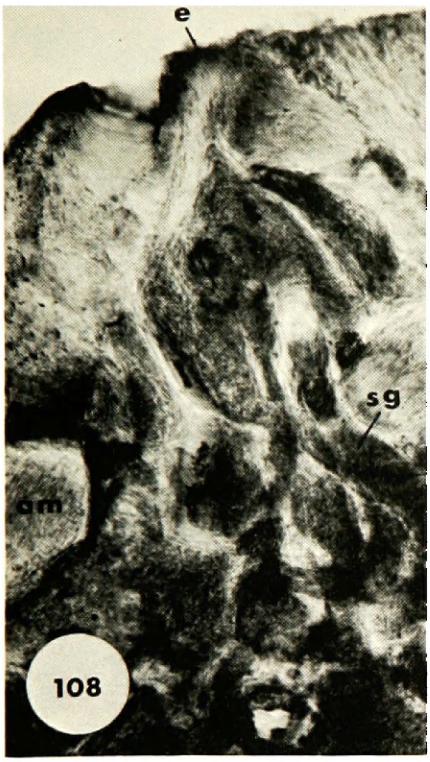
Figure 109. Median gland 69-1. Large long arrector pili muscles (am) associated with the hair follicle (hf). Reticular layer (rl). Approx. 84 X.

Figure 110. Median gland 69-1. Notice the small sebaceous acini (a), large arrector pili muscles (am), and the sebaceous excretory ducts (ed). Approx. 84 X.

Figure 111. The dilated apocrine tubules (at) that are typical of the median gland 69-1. The formation of the apocrine duct (ad). Approx. 84 X.

Figure 112. Median gland 69-1. Cuboidal epithelium (ce) lines the apocrine tubules. Dense connective tissue (dc) surrounds the tubules. Notice little secretory material in the lumen. Approx. 383 X.

Figure 113. Median gland 69-1. A few scattered regressed, atrophied and some regenerating associated apocrine cells (aa) are located in the dense connective tissue surrounding the tubules. Approx. 383 X.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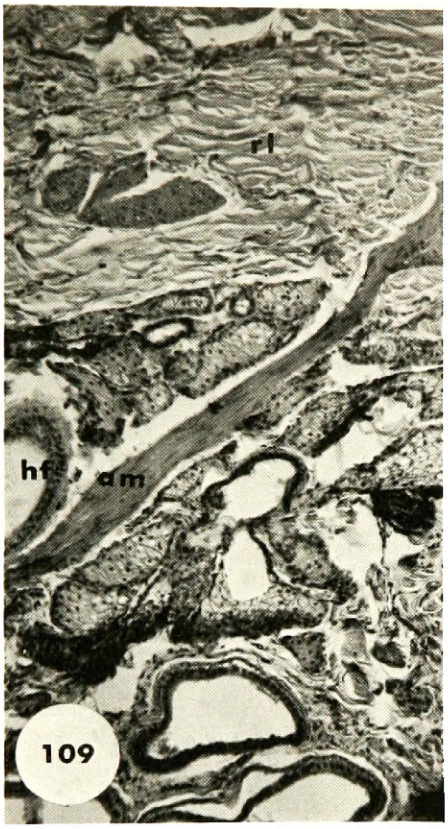
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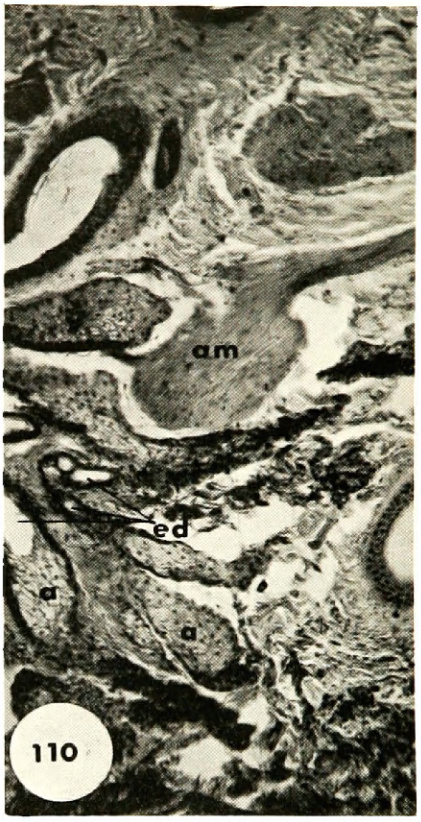
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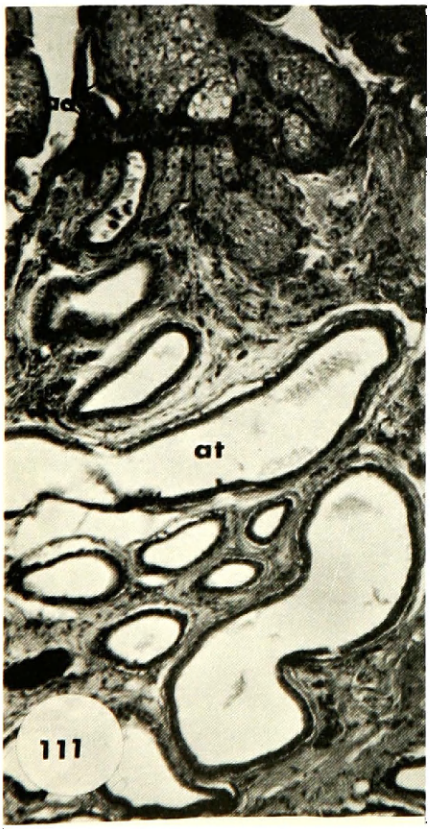
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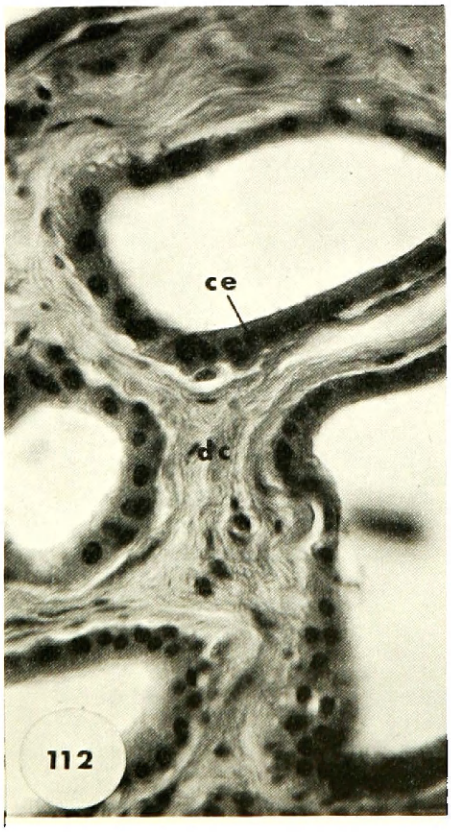
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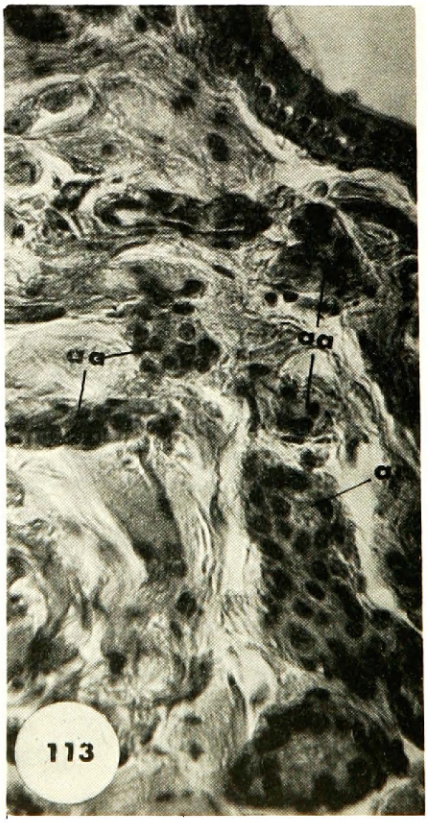
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scattered cytoplasmic buddings and the lumens have little secretory material, indicating slight secretory activity. Dense connective tissue with numerous fibroblasts surrounds the tubules (Figure 112). There also appear to be small clumps of regressed, atrophied, and some regenerating apocrine cells in the connective tissue that are typical of the sub-auricular gland (Figure 113).

The apocrine tubules emerge into a duct composed of simple cuboidal cells. As the duct approaches the hair follicle, the lining becomes stratified squamous, similar to the epidermal epithelium around the hair follicle. The duct empties into the pilosebaceous canal above the common sebaceous duct.

The inner zone, 0.11 mm. thick, is made up of dense collagenous tissue. Some large blood vessels are scattered throughout the gland but it is not as richly supplied as the rump gland.

The presence of some associated apocrine cells and the dilation of the apocrine tubules suggest that this gland might undergo seasonal variation. However, the examination of additional gland samples from different months is necessary to confirm this position.

The median gland "opens" or spreads its hairs when the rump hairs are erected so the function may be similar to that of the rump gland. If it is seasonal, it may add an "excited sex scent" besides being an additional airborne alarm scent.

SUMMARY

1. Glands of seventeen pronghorns (Antilocapra americana), collected during different months, were examined.

2. The subauricular gland exhibits abrupt glandular proliferation in the early spring. During the summer it enlarges and is highly secretory. There is a gradual regression and atrophy in the fall, and quiescence in December.

The apocrine cuboidal secretory cells of early spring gradually accumulate secretory material. Extensive cytoplasmic extension of the tall columnar secretory cells occurs in June. The peak of glandular activity occurs in August and is typified by tall mature sebaceous storage vessicles and large amounts of secretory material in the lumens of the tubules. Minute lipid vacuoles within the central cells of the acini combine to form large ~~vessicles~~ vacuoles prior to disintegration of their cell membranes.

Irregular clumps of associated apocrine cells begin to appear in January and February and are numerous in the summer. They gradually disappear during the fall and early winter and appear to be associated with apocrine secretory behavior.

3. The subauricular glands of castrated pronghorns are small and are relatively inactive compared to the normal pronghorns collected during the same month. The activity of the normal subauricular gland follows the cyclic testicular activity. This suggests that the glands are controlled by

gonadal hormones. The glands reach a climax in secretory activity in August just prior to the breeding season.

4. The subauricular skin patch from the female pronghorn has no resemblance to the subauricular gland of the male. It is similar to normal antelope skin.

5. The rump gland consists primarily of lobulated sebaceous units and coiled apocrine suboriferous tubules that maintain a constant, slight secretory activity throughout the year. The apocrine tubules and lumens are lined by tall columnar secretory epithelium, and the tubules appear more sudanophilic than those of the subauricular gland. Only minute lipid vacuoles accumulate in the central cells of the acini prior to disintegration of the cell membranes. Unusually large bundles of arrector pili muscles are associated with the hairs, which may allow for instant secretion as well as hair erection. The gland is richly supplied with blood vessels. The rump gland of the male, female, and castrated pronghorn are grossly and histologically similar. The rump gland appears to serve as an olfactory warning system complimentary to the visual warning system of the flashy rump patch. The pronghorns may also rub the scent on tall vegetation.

6. The fore- and hindfoot interdigital glands are grossly and histologically similar. They are not similar to the interdigital glands of other artiodactyls studied. The glands are shaped like large socks which open onto the

hairy skin surface through a single large duct, lined by a rough, thick epidermis. The glands consist primarily of large, highly active sebaceous units, enormous, common sebaceous ducts lined by thick epidermis, and a few scattered apocrine tubules. Large arteries, nerves and sensory corpuscles are present in the dorsal and ventral dermis that surrounds the glands. No smooth muscles or hair follicles are present. The interdigital gland may function primarily in leaving a scent trail for other members of the species.

7. The single median gland slightly resembles the rump gland in size and histology of the glandular components. Small, shallow hair follicles are thinly scattered throughout the gland. The sebaceous zone consists primarily of small, scattered, lobulated acini that surround the hair follicles. Unusually large arrector pili muscles are associated with the hair follicle and serve to force glandular secretion. A few small clumps of regressed, atrophied, and regenerating associated apocrine cells are in the connective tissue that surrounds the dilated apocrine tubules. The dilated tubules and associated apocrine cells suggest that seasonal variation may occur, similar to that demonstrated for the subauricular gland. The median gland may serve as an alarm or sex scent.

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APPENDIX A

Means, Standard Deviation and 95%

Confidence Level of the Standard Error
(Two times the standard Error)

of

The Diameter of the Apocrine Tubules

Lumens and the Cell Heights

for

All the Antelope Examined

TABLE I

Subauricular Apocrine Cell Height Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
62-1	27	12.85	2.45	.94
69-1	51	10.45	1.70	.47
62-8	57	18.94	2.94	.78
62-3	31	10.13	1.52	.55
62-5	59	14.98	2.12	.55
61-1	45	18.60	3.24	.97
61-2	39	21.62	3.30	1.06
61-3	38	15.76	4.59	1.49
61-4	68	17.12	3.31	.80
61-5	73	10.70	2.81	.66
61-6	31	14.87	3.12	1.12
61-7	35	12.91	2.67	.90
61-8	19	12.32	4.42	2.03
CH3082	29	12.03	1.97	.73
CH3561	21	15.62	1.86	.81

TABLE II

Subauricular Apocrine Tubule Diameter Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
62-1	27	54.70	7.25	3.33
69-1	31	47.48	14.13	5.08
68-2	31	82.00	14.70	5.28
62-3	21	76.81	13.46	5.87
62-4	33	91.12	9.66	3.36
61-1	29	93.21	13.29	4.62
61-2	20	99.25	13.39	5.99
61-3	25	76.84	20.00	8.00
61-4	37	80.19	12.87	4.23
61-5	46	75.46	12.94	3.82
61-6	20	68.20	14.55	6.51
61-7	20	69.95	18.40	8.22
61-8	12	45.25	8.02	4.75
CH3082	22	49.19	9.61	4.10
CH3561	22	51.04	9.24	3.94

TABLE III

Subauricular Apocrine Lumen Diameter Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
61-2	19	27.80	8.16	3.74
69-1	31	24.84	13.19	4.78
68-2	31	39.32	14.50	5.21
62-3	21	52.71	12.62	5.51
62-4	33	52.70	10.90	3.78
61-1	29	54.79	13.31	5.76
61-2	20	54.50	12.20	5.46
61-3	25	44.40	13.49	5.40
61-4	37	43.94	12.01	3.95
61-5	46	51.06	10.59	3.12
61-6	20	31.10	11.45	5.12
61-7	20	39.05	21.80	9.75
61-8	12	22.08	7.89	4.56
CH3082	22	21.73	7.94	3.39
CH3561	22	24.24	4.92	2.10

TABLE IV

Rump Apocrine Cell Height Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
62-1	49	20.16	2.94	.84
69-1	51	21.37	3.18	.89
68-2	56	22.75	4.61	1.23
61-1	52	18.56	2.27	.64
61-2	59	21.47	3.91	1.02
61-3	54	19.91	4.08	1.10
61-5	52	17.98	3.87	1.08
61-7	45	23.93	3.02	.90
61-8	53	22.92	3.39	.93
68-10	51	23.18	2.96	.83
CH3089	51	21.37	3.60	1.01
CH3082	51	22.16	4.61	1.29
CH3561	51	20.39	2.93	.82

TABLE V

Rump Apocrine Tubule Diameter Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
62-1	25	74.06	13.46	5.38
69-1	31	84.68	13.64	4.90
68-2	30	81.07	17.29	6.31
61-1	31	73.87	13.92	5.00
61-2	31	86.87	20.20	7.26
61-3	29	76.62	15.95	5.92
61-5	33	80.76	13.91	4.84
61-7	27	84.41	10.61	4.08
61-8	30	85.70	15.29	5.58
68-10	31	85.32	9.99	3.59
CH3089	31	88.39	20.50	7.36
CH3082	31	87.10	19.98	7.18
CH3561	31	78.71	14.10	5.06

TABLE VI

Rump Apocrine Lumen Diameter Measurements

Specimen Number	N	Mean (Microns)	Standard Deviation ±	95% Confidence Level ±
62-1	25	27.52	7.65	3.06
69-1	31	35.32	11.75	4.22
68-2	30	30.47	10.07	3.68
61-1	31	31.10	11.87	4.26
61-2	31	39.99	15.98	5.74
61-3	29	31.14	9.29	3.45
61-5	33	39.03	12.21	4.25
61-7	27	28.56	9.40	3.62
61-8	30	34.83	6.04	2.21
68-10	31	26.61	8.95	3.21
CH3089	31	35.00	13.64	4.90
CH3082	31	33.55	11.84	4.25
CH3561	31	29.03	8.50	3.05

APPENDIX B

Gross Glandular Measurements of the Fore- and Hindfoot Interdigital Glands

	Measurements					
	A	B	C	D	E	F
Forefoot Interdigital	16.8	15.5	13.1	3.5	52.6	23.3
Hindfoot Interdigital	16.9	8.9	11.1	2.2	55.5	31.6

Figure 1 has the explanation of measurements A-F.